

On two *Heptathela* species from southern Vietnam, with a discussion of copulatory organs and systematics of the Liphistiidae (Araneae: Mesothelae)

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On two *Heptathela* species from southern Vietnam, with a discussion of copulatory organs and systematics of the Liphistiidae (Araneae: Mesothelae). - *Songthela australis* Ono, 2002 is re-defined on the basis of new material from the type locality and from a second locality nearby. The male of this species is described for the first time. A closely related species, *Heptathela nui* sp. n., is described from males and females collected at two other localities in the same province. Variation in the copulatory organs of both species is illustrated and notes are given on their biology, particularly on their association with an ectoparasitic mite species of the genus *Ljunghia* Oudemans, 1932. "Twig-lining" is reported for one population of *H. nui* sp. n. *Songthela australis* and *H. nui* sp. n. are compared with *Nanthela tonkinensis* (Bristowe in Bristowe & Millot, 1933) and *H. tomokunii* Ono, 1997a from northern Vietnam, with *H. kimurai* (Kishida, 1920), *H. kikuyai* Ono, 1998, *Ryuthela owadai* Ono, 1997b and *R. nishihirai* (Haupt, 1979) from Japan, and with *Liphistius ornatus* Ono & Schwendinger, 1990 and *L. thaleri* Schwendinger, 2009 from Thailand. Additional taxonomic characters are illustrated for most of these species. Judging from apomorphies in the male copulatory organs, *S. australis* and *H. nui* sp. n. are sister species, but their female copulatory organs are very different. This challenges the generic concepts of *Songthela* Ono, 2000 and *Abcathela* Ono, 2000 (the latter earlier placed in the synonymy of *Heptathela*). The genus *Nanthela* Haupt, 2003 has no clear apomorphies, and transitions of diagnostic characters between *Nanthela*, *Songthela* and *Heptathela* were found. Thus *Nanthela* and *Songthela* are here placed in the synonymy of *Heptathela*. Morphology and conflicting terminology of copulatory organs in Liphistiidae, and the current confusion in Heptathelinae systematics are discussed. The copulatory organs of males and females of *Liphistius* Schiödt, 1849 and *Ryuthela* Haupt, 1983 are here considered as more derived than those of *Heptathela*. Some observations on moulting of liphistiid spiders are given.

Keywords: Taxonomy - new species - *Liphistius* - *Nanthela* - *Ryuthela* - *Songthela* - *Ljunghia* - Acari.

INTRODUCTION

The Heptathelinae (considered as a family by Haupt, 2003: 69) is a group of 41 species (including the new one described in here), which are very distinct in their genital morphology from the 49 currently known species of Liphistiinae (all in the genus *Liphistius*) and which are also geographically separated. Heptathelinae occur in eastern Asia, Liphistiinae in southeastern Asia, both ranges roughly divided (but not everywhere; Schwendinger, in preparation) by the river Mekong. Originally only comprising the genus *Heptathela* Kishida, 1923, other genera were added to the Heptathelinae as the number of species increased: *Ryuthela* Haupt, 1983, *Abcathela* Ono, 2000, *Songthela* Ono, 2000, *Vinathela* Ono, 2000, *Nanthela* Haupt, 2003 and *Sinothela* Haupt, 2003. Unfortunately many of the recently added genera were based on characters of a single sex.

The discovery of heptatheline spiders at four localities in Lam Dong Province, including the type locality of *Songthela australis*, by one of us (PJS) in 2003 yielded the previously unknown male of that species and a new, closely related one. With this also came a surprise: the male copulatory organs of both species are very similar, but the female copulatory organs so strongly different that, according to the current system, they would need to be placed in different genera. Thus an examination of additional heptatheline species had to be carried out to re-evaluate the existing generic concepts in this group, and this further revealed serious confusion in the terminology used to describe copulatory organs of liphistiid spiders in the literature.

MATERIAL AND METHODS

External morphology was studied and drawn with a Zeiss SV11 stereomicroscope, the vulvae (tissue removed with forceps) with a Nikon Optiphot compound microscope (both with a drawing tube). SEM micrographs were taken with a Zeiss DSM-940A scanning electron microscope; prosoma photos were taken at several focal planes with a digital camera on a Leica MZ APO stereomicroscope and assembled with the AutoMontage® system. Hairs were partly or completely omitted in the drawings of the male palp. Body measurements were taken with a stereomicroscope and are given in mm. The total body length includes the chelicerae. The carapace length was measured in a slightly forward-inclined position, with the anterior and the posterior margins at the same focal plane. Lengths of leg articles and palpal articles were measured on the dorsal side, from midpoint of anterior margin to midpoint of posterior margin, and are given in the following order: total (femur + patella + tibia + metatarsus + tarsus).

Terminology of the copulatory organs in Heptathelinae largely follows Song & Haupt (1984), but what they called “receptacles” (other authors called them bursae) are here called “receptacular clusters” (except for the *H. tomokunii* females examined). The term “genital plate” is inappropriate for Heptathelinae because that refers to the ventral wall of the genital atrium plus the entire bursa copulatrix with its dorsal and ventral walls, all of which are unsclerotised. “Sclerotised” refers to areas in the cuticle that are hard, stiff and strongly pigmented; “unsclerotised” refers to cuticular structures that are thin and unpigmented or thick and moderately pigmented (as is the bursa copulatrix) but that are always flexible. We use “cymbial projection” as a shorter form of Haupt’s (2003: 69) “distal projection on the ventral side (of the cymbium)”, which

can also be described as the “elongate proventral-distal lobe of the cymbium”. “Carapace” is used instead of “dorsal plate of prosoma”. The informal appellation “allotype” refers to the paratype on which the description of the female of the new species is based. Positioning (dorsal, ventral, etc.) on the palpal organ refers to an unexpanded, outstretched palp. In the following text generic names, which are currently in synonymy or which are here placed in synonymy, are given between inverted commas.

Abbreviations not explained in the figure legends are: AME, ALE, PME, PLE = anterior (posterior) median (lateral) eyes; IEBR = Institute of Ecology and Biological Resources of the Vietnamese Academy of Science and Technology, Hanoi, Vietnam; MHNG = Muséum d'histoire naturelle de la Ville de Genève, Switzerland; MOQ = median ocular quadrangle; MNHN = Muséum national d'Histoire naturelle, Paris, France; NSMT = National Museum of Nature and Science (formerly National Science Museum), Tokyo, Japan.

TAXONOMY

Liphistiidae Thorell, 1869

Heptathelinae Kishida, 1923

Heptathela Kishida, 1923

Abcathela Ono, 2000; type species *Heptathela abca* Ono, 1999; placed in the synonymy of *Heptathela* by Haupt, 2003: 71, 79.

Nanthela Haupt, 2003; type species *Liphistius tonkinensis* Bristowe in Bristowe & Millot, 1933; **syn. n.**

Sinothela Haupt, 2003; type species *Heptathela sinensis* Bishop & Crosby, 1932; placed in the synonymy of *Songthela* by Platnick, 2011 (in an earlier version of that online catalogue); **syn. n.**

Songthela Ono, 2000; type species *Heptathela hangzhouensis* Chen, Zhang & Zhu, 1981; placed in the synonymy of *Sinothela* by Haupt, 2003: 71; **syn. n.**

Vinathela Ono, 2000; type species *Heptathela cucphuongensis* Ono, 1999; placed in the synonymy of *Heptathela* by Haupt, 2003: 71, 79.

TYPE SPECIES: *Liphistius kimurai* Kishida, 1920.

EMENDED DIAGNOSIS: Distinguished from *Ryuthela* Haupt, 1983 by males possessing a conductor on sclerite III of the palpal organ and lacking an enlarged denticle (= contrategular spine) on its sclerite II; females with 2, 3 or 4 receptacles or receptacular clusters on the anterior margin of the bursa copulatrix (if 2, then these more widely separated from each other than in *Ryuthela*), or with 2 anteriorly and 2 dorsally on the bursa, or with 2 anteroventrally and 2 anterodorsally. Distinguished from *Liphistius* Schiödt, 1849 by the presence of 7-8 spinnerets (posterior medians more or less distinctly fused) and by the lack of clavate trichobothria on tarsi of legs and palps; males without retrolateral tibial apophysis on palp, palpal organ with large tegulum carrying two prominent apophyses, contrategulum and subtegulum without apophyses, paracymbium without cumulus; females with leathery but unsclerotised walls of the bursa copulatrix devoid of thickened rim and vesicles, gland pores usually restricted to receptacles or receptacular clusters situated anteriorly, dorsally or only slightly anteroventrally on the bursa.

THE TWO SPECIES FROM SOUTHERN VIETNAM

Heptathela australis (Ono, 2002)

Figs 1-20, 55-58, 67

Songthela australis Ono, 2002a: 120-122, figs 1-8 (description of female).*Heptathela australis* (Ono, 2002).- Platnick, 2011 (transferred without explanation in an earlier version of that online catalogue; this generic placement is maintained here).

MATERIAL EXAMINED: NSMT-Ar 9617 (1 male), IEBR, without registration numbers (1 male and 1 female), MHNG, without registration numbers (all other specimens), sample SV-03/18; 9 males (matured early June 2004, 2.VII.2004, 30.VII.2004, 30.VI.2006, 10.V.2007, 24.V.2007, May 2007, 17.IV.2008, 27.IV.2008), 10 females and 1 juvenile; near Dambri Waterfall, about 18 km N of Bao Loc, 11°38'42"N, 107°44'37"E, 850 m; 1.-2.IX.2003; leg. P. J. Schwendinger. – MHNG, without registration number, sample SV-03/17; 1 male; Lam Dong Province, off the road from Da Hoa (= Da Huoi) to Bao Loc, about 13 km SW of Bao Loc, 11°27'20"N, 107°43'04"E, 690 m; 31.VIII.2003; leg. P. J. Schwendinger.

EMENDED DIAGNOSIS: Males of *H. australis* differ from those of *H. tonkinensis* by a narrower cymbium with a longer and narrower elongate proventral-distal projection; paracymbium much longer and basally much narrower, almost forming a right angle with the cymbium; an unpigmented and unsclerotised zone present distoventrally on cymbium; marginal tegular apophysis much longer and pointed, terminal tegular apophysis with its dorsal edge much less projecting and less dentate; contrategulum with two distal edges running parallel to each other: an outer sharp edge and an inner dentate edge; the sharp edge with a pronounced, beak-like extension prolaterally, the dentate edge not connected with the isolated denticles in the ventro-proximal part of the contrategulum; conductor shorter, situated close to the embolus, its apex without denticles; embolus longer. Females of *H. australis* are similar to those of *H. hangzhouensis*, differing by larger posterior "bursae" (= receptacular clusters) (see Ono, 2002a: 120, referring to Song & Haupt, 1984: fig. 3c-d). Another distinction is found in the shape of the bursa copulatrix in dorsal and ventral view: longer and trapezoidal or triangular in *H. australis*, shorter and rectangular in *H. hangzhouensis*.

DESCRIPTION OF MALE (matured 10.V.2007): Colouration in alcohol (live specimens distinctly darker): Ground colour of carapace light brown, with indistinct dark brown W-shaped pattern behind dark ocular mound and with dark brown band along anterior and lateral margins. Opisthosoma cream, mottled with light grey; tergites uniformly light greyish brown; sternites light orange-brown; spinnerets cream. Chelicerae light brown distally, cream proximally. Legs and palps dorsally uniformly light reddish brown except for a dark red-brown distal zone of the cymbium (not including cymbial projection); no dark annulation present. Ventral side of body and limbs generally lighter than dorsal side.

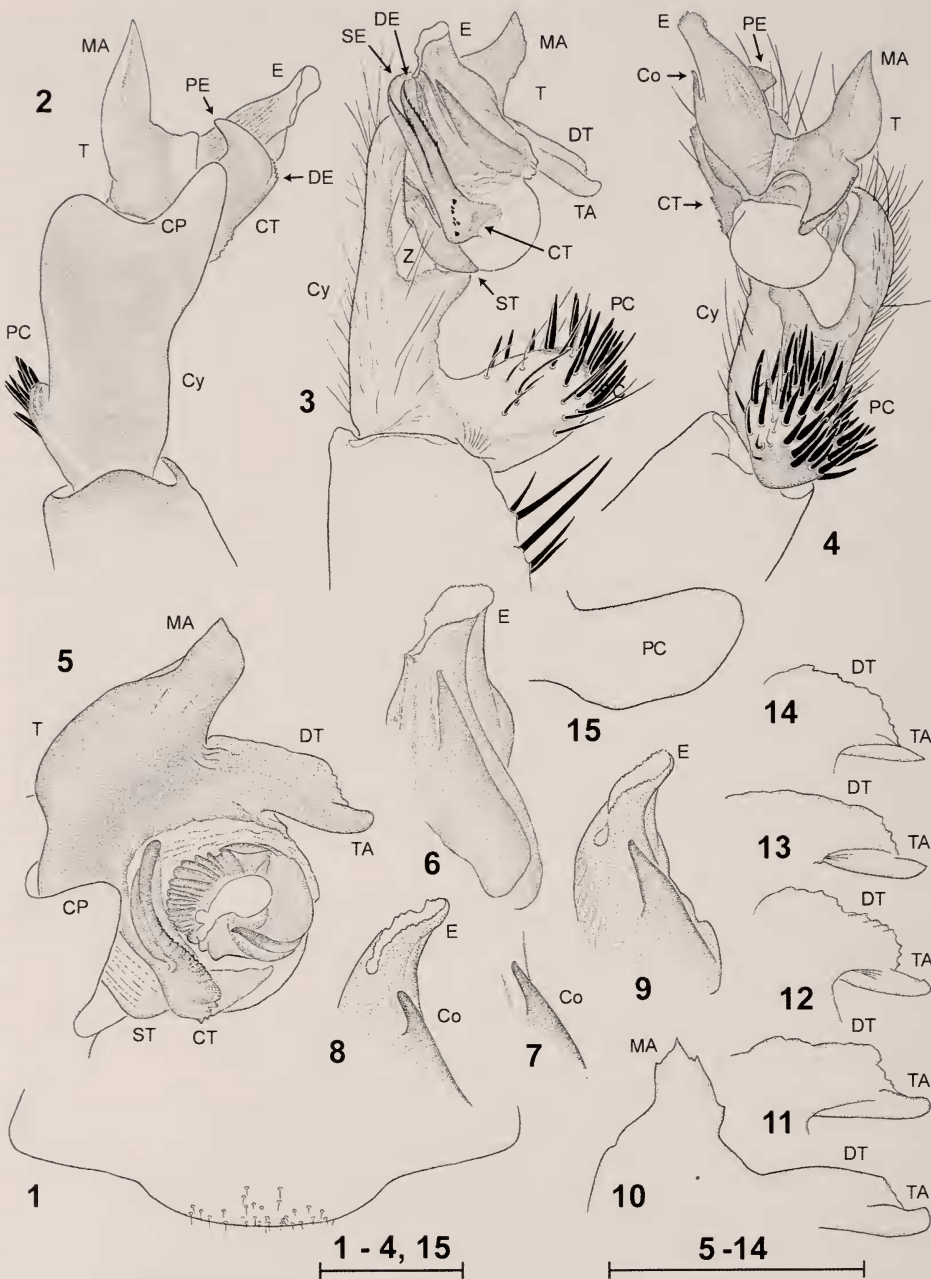
Total length 15.2. Carapace 6.4 long, 5.2 wide, set with a few short, peg-like hairs (with blunt tips) on margin (mostly anteriorly and posteriorly), behind ocular mound and on coxal elevations, only few longer pointed hairs running over ocular mound in a longitudinal row. Eye group 0.92 long, 1.05 wide. Eye sizes and interdistances: AME 0.04, ALE 0.59, PME 0.30, PLE 0.53; AME-AME 0.09, AME-ALE 1.14, PME-PME 0.04, PME-PLE 0.12, ALE-PLE 0.08. MOQ 0.43 long, front width 0.19, back width 0.46. Labium 0.4 long, 1.2 wide. Sternum 2.5 long, 2.2 wide (1.2 on ventral surface). Anterior margin of sternum distinctly elevated, thus a deep suture present between sternum and labium. Maxillae 2.2 long, 1.4 wide. Promargin of cheliceral

groove with 10 small teeth on each chelicera. Paired tarsal claws with 4-5 teeth; unpaired claws without denticles. Measurements of limbs: palp 11.4 (3.4 + 1.9 + 3.9 + 2.2); leg I 18.7 (5.1 + 2.4 + 3.8 + 4.9 + 2.5); leg II 19.1 (5.0 + 2.4 + 3.7 + 5.3 + 2.7); leg III 20.4 (4.9 + 2.5 + 3.8 + 6.2 + 3.0); leg IV 26.5 (6.5 + 2.7 + 5.0 + 8.6 + 3.7). "Tibial spurs" (sensu Platnick & Goloboff, 1985) absent on all legs. Opisthosoma 5.7 long, 3.6 wide; posterior margin of genital sternite (= sternite of second opisthosomal segment) widely rounded, with slightly protruding median part (Fig. 1).

Palp (Figs 2-15) with a quite long and narrow cymbial projection (Fig. 2); distoventral zone of cymbium (below subtegulum) unpigmented and unsclerotised, formed by extension of unpigmented and unsclerotised inner (retrolateral distal) side of cymbium onto its ventral side (Fig. 3); paracymbium relatively long and narrow, with only indistinct proximal tubercle; cymbium and paracymbium almost at right angles (Fig. 3). Tegulum with two large apophyses: 1) marginal apophysis long, pointed, distad-directed, with a sharp edge running across it from prolateral to retrolateral side (Figs 2-4); 2) terminal apophysis retrolaterad- and slightly proximad-directed, with an abruptly narrowed and slightly distad-bent apex (Fig. 3), dorsal side of apophysis only moderately extended and carrying a low, weakly dentate edge, dorsal and ventral sides of apophysis almost parallel to each other (Figs 3, 5, 10-14); edges of both apophyses not in contact with each other. Contrategulum with a few isolated denticles ventro-proximally and with two parallel distal edges, the outer one sharp, the inner one finely dentate, both uniformly pigmented (Fig. 3); sharp edge prolaterally abruptly truncate, with a beak-like extension pointing toward marginal apophysis of tegulum (Fig. 2). Conductor arising ventro-proximally on embolus (= bulbal sclerite III), its proximal half fairly wide and fused with base of embolus, its distal half free, blade-like, with continuously narrowing sides and pointed apex (Figs 3-9). Embolus largely sclerotised, prolateral half strengthened by numerous longitudinal ribs (Figs 2-5); terminal fringe around opening of sperm duct (= spermophore) hyaline and finely serrate (Figs 3-4, 6, 8-9).

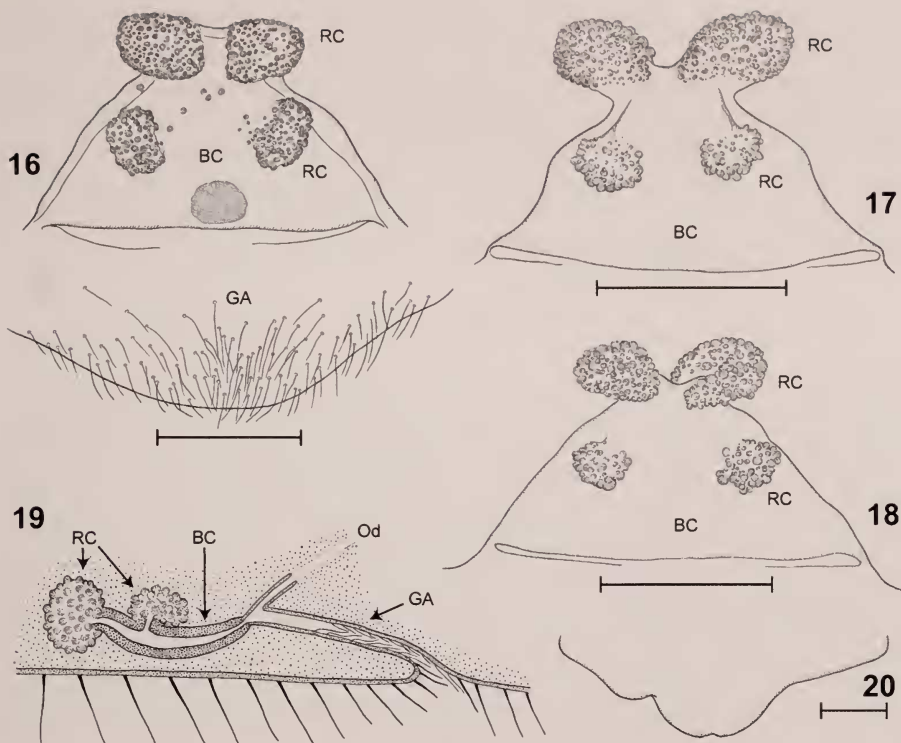
DESCRIPTION OF FEMALE: See Ono (2002a: 120-122, figs 1-8). Anterior margin of sternum elevated as in male, thus also with a deep suture between sternum and labium. "Tibial spurs" present on legs I-III. Vulva as in Figs 16-19, 55-58.

VARIATION: Range of measurements in males (n=10) and in newly collected females with clearly developed vulva (n=10; in parentheses): body length 12.7-17.6 (15.3-24.1), carapace length 5.4-7.1 (6.0-9.4), carapace width 4.2-6.2 (4.8-8.1). Variation in the overall shape of the vulvae of four new females is not strongly pronounced (Figs 16-18, 55). The largest female (only it) has a dark brown spot on the ventral wall of the bursa copulatrix, and several small sclerotised vesicles (as the ones on the receptacular clusters), penetrated by gland pores, sitting on the dorsal wall of the bursa copulatrix, in between the four receptacular clusters (Fig. 16). The latter character can be an atavism (see Discussion: evolution of female copulatory organs). In one female the posterior margin of the genital sternite is indented (probably from an injury sustained in an earlier instar; Fig. 20). For variation in the shape of the palpal organ, see Figs 6-9 (conductor), Figs 3, 10 (marginal tegular apophysis) and Figs 5, 10-14 (terminal tegular apophysis). One male has a proximally narrow paracymbium (Fig. 15). The number of isolated denticles ventro-proximally on the contrategulum varies from 2-7.



FIGS 1-15

Heptathela australis (Ono, 2002), male (mature 10.V.2007) from the type locality (1-6), five other males from the type locality (7, 11; 9; 10; 12; 13), male from Dao Hoa - Bao Loc (8, 14-15). (1) Posterior margin of genital sternite, ventral view. (2) Distal part of left palp, prolateral view. (3) Same, ventral view. (4) Same, retrolateral view. (5) Same, distal view. (6, 8-9) Embolus and conductor, proventral view. (7) Conductor, proventral view. (10) Marginal and terminal apo-



FIGS 16-20

Heptathela australis (Ono, 2002). (16) Vulva of largest female, dorsal view; dorsal and lateral walls of genital atrium not shown. (17-18) Bursae copulatrix of two other females, dorsal view. (19) Schema of vulva, lateral view (the oviduct is actually anterodorsad- and not posterodorsad-directed). (20) Posterior margin of deformed genital sternite, ventral view. BC = bursa copulatrix; GA = genital atrium; Od = oviduct; RC = receptacular cluster. Scale lines 1.0 mm.

RELATIONSHIPS: Despite pronounced differences in female copulatory organs, *H. australis* appears most closely related to *N. nui* sp. n. Their palps share distinct synapomorphies, and both species occur in the same mountain range, about 80 km apart. Their closest known relatives are *H. tonkinensis* and *H. tomokunii* from northern Vietnam, but more closely related species most likely await discovery in the mountains between Da Lat and Hanoi. The male of the geographically closer *H. cucphuongensis* (from south of Hanoi) is unknown and therefore the relationships of this species are not yet clear.

physis of tegulum, ventral view. (11-14) Terminal apophysis of tegulum, ventral view. (15) Outline of paracymbium, ventral view. Co = conductor; CP = cymbial projection; CT = contrategulum; Cy = cymbium; DE = dentate distal edge of contrategulum; DT = dorsal extension of terminal apophysis of tegulum; E = embolus; MA = marginal apophysis of tegulum; PC = paracymbium; PE = prolateral extension of sharp distal edge of contrategulum; SE = sharp distal edge of contrategulum; ST = subtegulum; T = tegulum; TA = terminal apophysis of tegulum; Z = unpigmented distoventral zone of cymbium. Scale lines 1.0 mm.

DISTRIBUTION: Known only from two localities near Bao Loc village in southern Vietnam.

BIOLOGY: The mature male was discovered when scraping leaf litter from the floor of an evergreen broadleaf forest. He probably had left his burrow in search of females and was taking temporary shelter in the leaf litter during the day. All other spiders were extracted from their burrows in sun-exposed earth banks (with little vegetation) on one side of a dirt road in an old secondary forest. None of the burrows inspected at the beginning of September contained mature males, and by then the mating period was probably at its end.

All burrows were closed with a single trapdoor that had its hinge on the upper side of the entrance; the lower rim of the burrow entrance was slightly protruding. Trapdoors of females were up to 3.3 cm wide and 2.5 cm long; those of penultimate males 2.0-2.3 and 1.5-1.8 cm, respectively. No spiders were seen when their doors were carefully opened with forceps for inspection. They were resting in the depth of their burrows and could not be provoked to come to the entrance by inserting a flexible grass stem and disturbing them (which often works for extracting spiders of the genus *Liphistius*). All these spiders had to be dug up. Large and medium-sized spiders (including adult males) react to disturbance by repeatedly raising their body above the ground while the leg tarsi remained on the ground (a behaviour called "tiptoeing") and by spreading their chelicerae, as large *Liphistius* also do. Four egg cases (2.5-3.5 cm in diameter and 1.4-1.9 cm high) were built between the end of November and late December 2003. Three of them held clusters of 129-164 beige or light yellow eggs wrapped in a thin skin made of a coagulated vulval secretion and some fine silken threads (as present in all liphistiid egg cases examined, but less distinct in *Liphistius*), resting on a mesh of fine threads above the bottom of the inner chamber of the egg case. Ninety-nine third (or later?) instar juveniles were taken from the fourth egg case in mid-April 2004. Five of them were males that reached maturity in June 2006, May 2007 and April 2008, which is presumably earlier in the year than in nature (since the adult male was found at the end of August). Development from eggs to adult males in captivity thus took between one and a half years and three years and four months. Females which laid eggs between November and December moulted in the following March, May and June.

Three of the large females, which were collected in the field and subsequently laid eggs in Geneva, each carried more than 50 ectoparasitic mites of different instars on their prosoma. These mites were usually sitting on the carapace, but when disturbed took shelter on the ventral side, between the coxae and the sternum, and between the prosoma and the opisthosoma. They pierced the carapace at numerous places and left clearly visible dark round scars that make the spiders look as if they had measles (Fig. 67). The carapace, a quite strongly sclerotised plate, is an unlikely place for sucking body fluids. Surprisingly, no scars or any other signs of damage are visible on the soft membranes between the sclerites of the prosoma or on the opisthosoma.

Heptathela nui sp. n.

Figs 21-33, 68

HOLOTYPE: MHNG, without registration number, sample SV-03/21; male (matured 10.VI.2004); Vietnam, Lam Dong Province, Mt Penhatt near Quang Trung Reservoir, about 8 km SW of Da Lat, 11°52'37"N, 108°25'58"E, 1500 m; 6.IX.2003; leg. P. J. Schwendinger.

PARATYPES: MHNG, without registration number, sample SV-03/21; 2 males (matured 3.V.2004, 10.VII.2004) and 3 females ("allotype" constructed egg case in XII.2003 and moulted 5.IV.2004); collected together with the holotype. – NSMT-Ar 9618, 9619 (1 male, 1 female), IEBR, without registration numbers (1 male, 1 female), MHNG, without registration numbers (all other specimens), sample SV-03/22; 3 males (matured early June 2004, 15.VI.2004, 21.IV.2005) and 4 females; Cam Ly Waterfall, western outskirts of Da Lat city, 11°56'37"N, 108°25'14"E, 1450 m; 8.-9.IX.2003; leg. P. J. Schwendinger.

ETYMOLOGY: "Nui", a noun in apposition, is the Vietnamese word for "mountain".

DIAGNOSIS: Males of the new species can be distinguished from those of the closely related *H. australis* by: anterior margin of sternum low; paracymbium stronger, with distinct proximal tubercle; conductor narrower, with more strongly bent apex; tegulum with larger marginal apophysis, terminal apophysis more continuously narrowing towards apex, its dorsal and ventral sides at an acute angle to each other; prolateral side of contrategulum with light-coloured central portion; sharp (outer) distal edge of contrategulum convex, broadly rounded, without beak-like extension; denticles on inner edge of contrategulum running down to ventro-proximal area in a continuous row; embolus shorter, its terminal fringe more coarsely serrate. Females of *H. nui* sp. n. differ from those of *H. australis* by: bursa copulatrix shorter, with more strongly inclined lateral margins; receptacular clusters smaller, with more or less distinct stalks, all four sitting on the anterior margin of the bursa copulatrix.

DESCRIPTION: MALE (holotype). Colouration in alcohol (live specimens distinctly darker): Carapace and legs light reddish brown; ocular mound dark; bulbal sclerites and distal part of cymbium red-brown, cymbial projection light brown. No annulation on legs or dark pattern on carapace and opisthosomal tergites. Ventral side of body and limbs generally lighter than dorsal side. Opisthosoma cream, mottled with light grey; tergites uniformly light greyish brown.

Total length 14.4. Carapace 6.3 long, 5.0 wide, set with a few short, peg-like hairs (with blunt tips) on margin (mostly anteriorly and posteriorly), behind ocular mound and on coxal elevations; only few long pointed hairs running over ocular mound in a longitudinal row. Eye group 0.87 long, 0.99 wide anteriorly, 0.91 posteriorly. Eye sizes and interdistances: AME 0.04, ALE 0.60, PME 0.32, PLE 0.50; AME-AME 0.14, AME-ALE 0.07, PME-PME 0.05, PME-PLE 0.08, ALE-PLE 0.06. MOQ 0.43 long, front width 0.21, back width 0.52. Labium 0.5 long, 1.2 wide. Sternum 2.7 long, 2.2 wide (1.3 on ventral surface). Anterior margin of sternum low, thus only a shallow furrow present between sternum and labium. Maxillae 2.2 long, 1.4 wide. Promargin of cheliceral groove with 10 teeth on right chelicera, 12 on left. Paired tarsal claws with 3-5 teeth; unpaired claws without denticles. Measurements of limbs: palp 12.1 (3.6 + 2.1 + 4.1 + 2.3); leg I 19.7 (5.6 + 2.5 + 4.0 + 5.0 + 2.6); leg II 19.3 (5.2 + 2.4 + 3.8 + 5.2 + 2.7); leg III 20.6 (5.0 + 2.5 + 3.8 + 6.2 + 3.1); leg IV 25.9 (6.6 + 2.7 + 4.9 + 8.2 + 3.5). "Tibial spurs" absent on all legs. Opisthosoma 5.6 long, 3.7 wide; posterior margin of genital sternite widely rounded, with an indistinct invagination in the middle (Fig. 21).

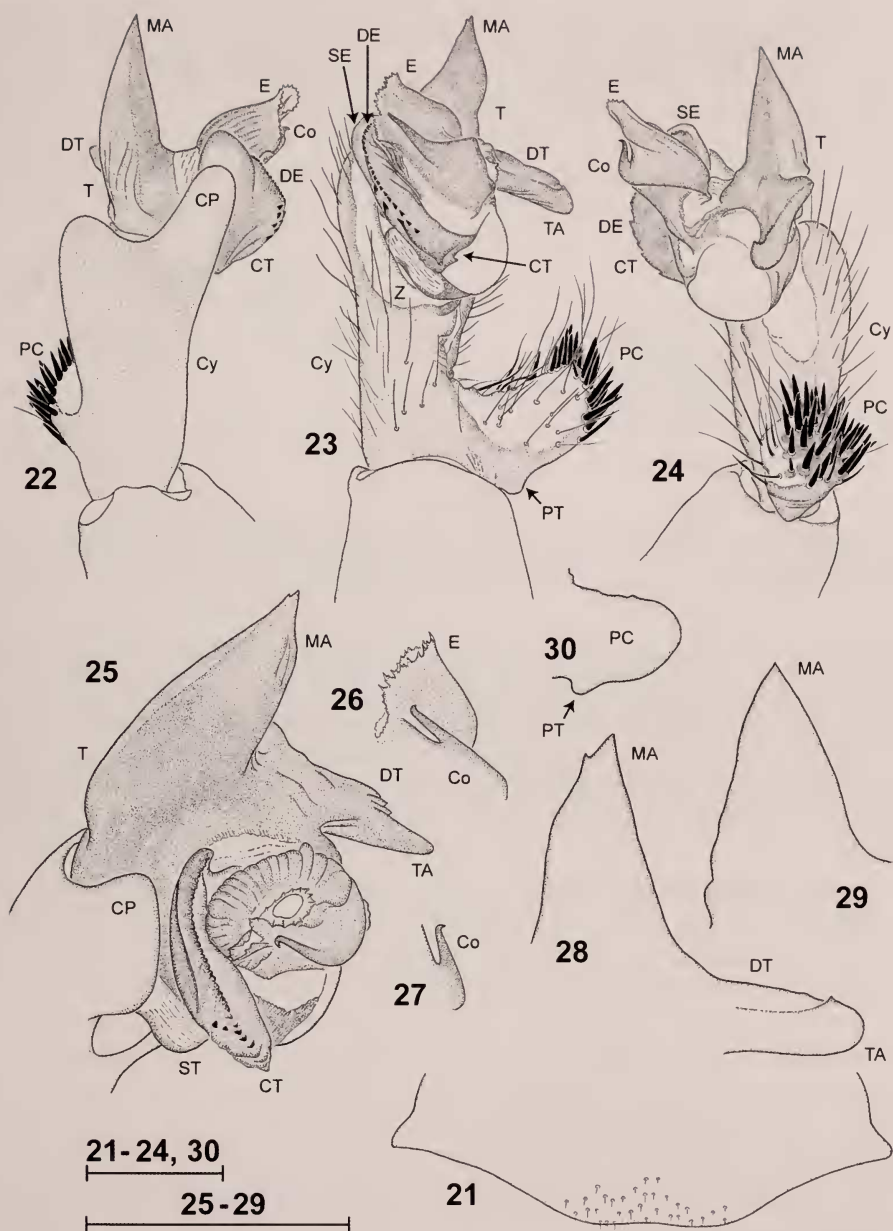
Palp (Figs 22-26) with paracymbium carrying a proximal tubercle (Fig. 23); cymbium and paracymbium almost at right angles to each other; distoventral zone of cymbium (below subtegulum) unpigmented and unsclerotised (Fig. 23). Tegulum with a very long, pointed, distad-directed marginal apophysis with a sharp edge (Figs 22-25), and with a retrolaterad- and slightly proximad-directed terminal apophysis continuously narrowing to a rounded, distad-bent apex (Figs 23, 25); dorsal side of terminal apophysis less extended than in *H. australis*, carrying a weakly dentate edge (Fig. 25) not being in contact with edge on marginal apophysis. Contrategulum with a cream central portion on prolateral side (Fig. 22); two parallel distal edges present: the outer one sharp, the inner one finely dentate (Fig. 23); sharp edge convex, widely rounded, without beak-like extension (Fig. 22); row of denticles on inner edge running down to near ventro-proximal margin of contrategulum and there forming two rows of denticles together with a few irregularly arranged additional denticles situated more proximally (Fig. 23). Conductor situated ventro-proximally on embolus; proximal portion of conductor fairly wide and fused with embolic base; distal portion of conductor free, narrow, blade-like, with slightly hook-like apex (Figs 23-26). Embolus largely sclerotised, prolateral half strengthened by numerous longitudinal ribs (Figs 22, 25); terminal fringe around opening of sperm duct (= spermophore) hyaline, coarsely serrate, with fairly deep indentations (Figs 22-24, 26).

FEMALE ("allotype"). Colouration similar to that of male but slightly lighter; palpal tarsi brown.

Total length 21.6. Carapace 8.3 long, 6.3 wide. Eye group 0.97 long, 1.03 wide anteriorly, 1.00 posteriorly. Eye sizes and interdistances: AME 0.06, ALE 0.60, PME 0.35, PLE 0.50; AME-AME 0.19, AME-ALE 0.14, PME-PME 0.04, PME-PLE 0.06, ALE-PLE 0.06. MOQ 0.49 long, front width 0.30, back width 0.52. Labium 1.1 long, 2.0 wide. Sternum 3.6 long, 2.5 wide (1.9 on ventral surface), its anterior margin distinctly elevated, thus separated from labium by a deep suture (not so in males). Maxillae 2.8 long, 1.9 wide. Promargin of cheliceral groove with 11 teeth on each chelicera. Paired tarsal claws of legs with 2-4 teeth, unpaired claws without denticles; each palpal claw with 2 denticles. Measurements of limbs: palp 13.3 (4.5 + 2.5 + 3.0 + 3.3); leg I 15.2 (4.9 + 2.6 + 3.0 + 3.0 + 1.7); leg II 14.6 (4.4 + 2.6 + 2.7 + 3.1 + 1.8); leg III 15.5 (4.3 + 2.7 + 2.7 + 3.8 + 2.0); leg IV 21.9 (6.1 + 3.0 + 3.9 + 6.2 + 2.7). "Tibial spurs" present on legs I-III. Opisthosoma 7.7 long, 6.4 wide. Posterior margin of genital sternite broadly rounded, with a slight median invagination.

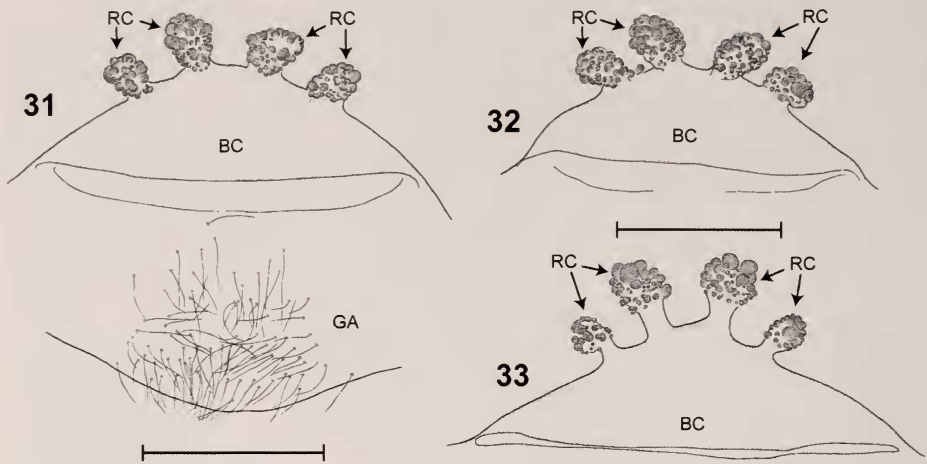
Vulva (Fig. 31). Bursa copulatrix short, plano-convex in dorsal and ventral view, its anterior margin widely rounded and carrying four anteriad-directed receptacular clusters on indistinct short stalks, the median pair slightly larger than the lateral one. Genital atrium densely set with fine hairs on dorsal and ventral walls.

VARIATION: Range of measurements in males (n=6) and in females with clearly developed vulvae (n=7; in parentheses) examined: Body length 13.2-16.5 (16.4-22.5), carapace length 5.2-6.5 (6.1-8.2), carapace width 4.2-5.3 (4.9-6.5). For variation in the shape of the vulva in three females, see Figs 31-33. In one female the receptacular clusters are raised on relatively long stalks (Fig. 33), in two other females the stalks are stout and rather indistinct (Figs 31-32). Variation in the shape of the palpal organ is less pronounced than in *H. australis*: the marginal tegular apophysis carries a subterminal



FIGS 21-30

Heptathela nui sp. n., male holotype (21-26) and three male paratypes from Cam Ly Waterfall (27-28; 29; 30). (21) Posterior margin of genital sternite, ventral view. (22) Distal part of left palp, prolateral view. (23) Same, ventral view. (24) Same, retrolateral view. (25) Same, distal view. (26) Embolus and conductor, proventral view. (27) Conductor, proventral view. (28) Marginal and terminal apophysis of tegulum, ventral view. (29) Marginal apophysis of tegulum, ventral view. (30) Outline of paracymbium, ventral view. PT = proximal tubercle of paracymbium; other abbreviations as in Figs 1-15. Scale lines 1.0 mm.



FIGS 31-33

Heptathela nui sp. n., three female paratypes. (31) Vulva of "allotype", dorsal view; dorsal and lateral walls of genital atrium not shown. (32-33) Bursae copulatricae of two other females, dorsal view. Abbreviations as in Figs 16-20. Scale lines 1.0 mm.

denticle in two males (Figs 25, 28), in others it is bare (Fig. 29); the proximal tubercle of the paracymbium is very distinct in two males (Figs 23, 30), less so in others; in some males the scattered denticles below the continuous row of denticles on the ventro-proximal side of the contrategulum are indistinct. In one female the posterior median spinnerets are fused only along their ental sides but the apices are still free, whereas in all other conspecific spiders examined these spinnerets are completely fused.

REMARKS: The paired leg claws of the "allotype" are inflated, especially on the posterior legs. This is not so in any of the other specimens of both species examined and thus it was probably caused by preservation. Similar rare cases of inflated claws were also observed in alcohol-preserved specimens of mygalomorph spiders.

RELATIONSHIPS: *Heptathela nui* sp. n. possesses a vulva similar to that of *H. abca* from northern Vietnam, and to *H. bristowei* Gertsch, 1967, *H. sinensis* and *H. schensiensis* (Schenkel, 1953) from central China. However, strong similarity and several likely synapomorphies in the male palps of *H. australis* and *H. nui* sp. n. show that these species are the most closely related. See also Discussion - Systematics.

DISTRIBUTION: Known only from two localities near Da Lat city in southern Vietnam.

BIOLOGY: The spiders examined were collected from a steam bank in an ever-green hill forest, from the recess of an earth bank at the side of a path in a pine forest (both at Mt Penhatt), and from an earth bank in a park with pine trees (at Cam Ly Waterfall). Burrows were as those of *H. australis*, but at the Cam Ly site (not so on Mt Penhatt) they all had several grass stems attached to their entrances to enlarge the sensory area. "Twig-lining" is known from individual populations of several species of

mygalomorph trapdoor spiders in Australia, North America and Japan (see Haupt, 1995 for a summary), and it was also reported for *Ryuthela* populations (Haupt, 1983: 286) and for some *H. abca* at the type locality (Ono, 1999: 41, figs 13-14). Trapdoors of females were up to 2.6 cm wide and 2.0 cm long; those of penultimate males 1.6-2.1 and 1.1-1.6 cm, respectively. Large and medium-sized spiders react to disturbance by “tiptoeing”, spreading their chelicerae and raising their palps. One egg case (2.5 cm in diameter and 1.7 cm high) was built on 19.XII.2004. It held 83 light yellow eggs suspended above the bottom of the inner chamber. The female with eggs moulted in early April of the following year; other females moulted in January, March, April, September, October and November, usually twice per year. Males (collected in early September 2003) became adult between May and July 2004 and in April 2005.

The largest female (gravid; died before laying its eggs) had about 50 ectoparasitic mites of the genus *Ljunghia* on its prosoma. These caused the same kind of scars on the carapace of the spider (Fig. 68) as described earlier in this paper for *H. australis*.

SPECIES EXAMINED FOR COMPARISON

Heptathela tonkinensis (Bristowe, 1933)

Figs 34-38

Liphistius birmanicus Thorell, 1897.- Simon, 1909: 70-71 (misidentification; description of male).

Liphistius tonkinensis Bristowe in Bristowe & Millot, 1933: 1022, text-fig. 4 (naming of species; illustration of palp of male holotype).- Bristowe, 1976: 4 (listing).

Heptathela tonkinensis (Bristowe, 1933).- Haupt, 1983: 284-285, figs 8a-b, d, 13e (transfer; description and illustration of palp of male holotype); Platnick & Sedgwick, 1984: 3 (transfer).

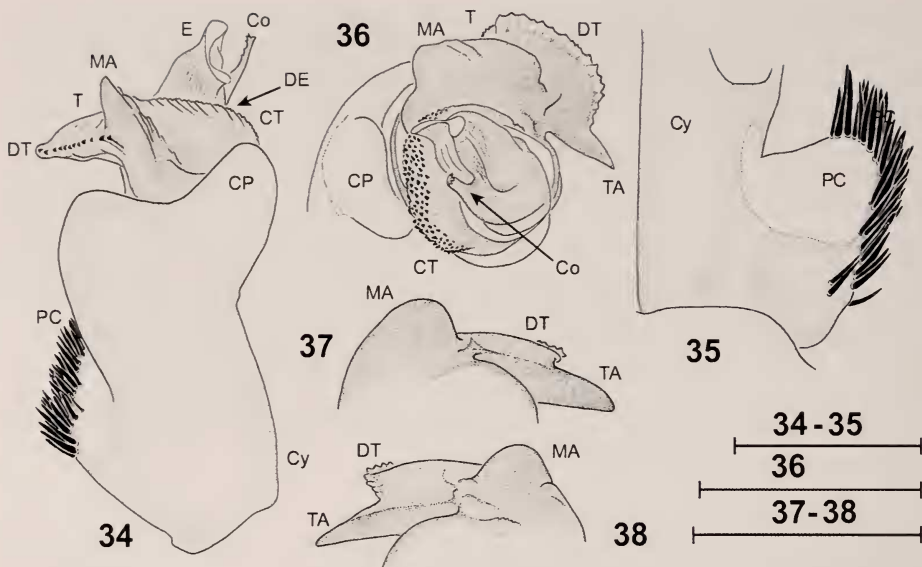
Vinatela tonkinensis (Bristowe, 1933).- Ono, 2000: 150 (transfer).

Nanthela tonkinensis (Bristowe, 1933).- Haupt, 2003: 69, 71, figs 51a-b (transfer; illustration of palp of male holotype).

Here transferred back to *Heptathela*.

MATERIAL EXAMINED: MNHN 29170, AR-4104; male holotype; Vietnam, Tonkin, forêt de Khà là; no collecting date; leg. Blaise.

EMENDED DIAGNOSIS: The previously published descriptions of the holotype do not mention some of the following characters: cymbial projection quite broad and distinctly inclined from axis of cymbium (Fig. 34); distoventral zone of cymbium (below subtegulum) pigmented and sclerotised as normal; paracymbium short and exceptionally wide at base, at an acute angle to axis of cymbium (Fig. 35); contrategulum distally with a broad band of denticles (arranged in several irregular rows) running down to near ventro-proximal margin of contrategulum, no sharp distal edge present (Fig. 36); marginal apophysis of tegulum fairly short, compressed and arched, with a sharp distal edge running from prolateral to retrolateral side (Figs 34, 37-38); terminal apophysis of tegulum beak-like, dorsally with a large and broadly arched extension with a coarsely dentate edge (Figs 34, 36-38) not in contact with edge on marginal apophysis; conductor long (about as long as embolus), its distal part fairly distant from embolus (Figs 34, 36). “Tibial spurs” absent on all legs. Posterior margin of genital sternite widely and uniformly rounded, without protruding median part. Anterior margin of sternum not markedly elevated, suture to labium therefore shallow (as in male of *H. nui* sp. n.).



FIGS 34-38

Heptathela tonkinensis (Bristowe, 1933), male holotype. (34) Distal part of left palp, prolateral view. (35) Paracymbium of left palp, ventral view. (36) Left palpal organ, distal view. (37) Marginal and terminal apophysis of tegulum of left palp, ventral view. (38) Same, right palp. Abbreviations as in Figs 1-15. Scale lines 1.0 mm.

REMARKS: The retrolateral view of the right palp of the holotype given by Bristowe (Bristowe & Millot, 1933: text-fig. 4) is detailed and correct, but it gives the false impression of a quite long and pointed marginal tegular apophysis, as present in *H. australis* and *H. nui* sp. n. A comparison of these three species showed that all of them have a fairly sharp distal edge on their marginal tegular apophysis, and in pro- and retrolateral view this apophysis always looks pointed (see also Fig. 34). Ventral and dorsal views show that in *H. tonkinensis* this apophysis is actually scale-like, fairly short and moderately arched (Figs 37-38; Haupt, 1983: fig 8b; Haupt, 2003: fig. 51B), whereas in *H. australis* and *H. nui* sp. n. it is long, triangular and truly pointed (Figs 3, 5, 10, 23, 25, 28-29).

RELATIONSHIPS: Among the heptatheline species of which males are known, *H. tonkinensis* currently appears most closely related to *H. tomokunii*; both are more distantly related to *H. australis* and *H. nui* sp. n. *Heptathela cuephuongensis* (known only from females), which also occurs in northern Vietnam (south of Hanoi), is geographically closer and possibly also more closely related to *H. tonkinensis* and *H. tomokunii* than to *H. australis* and *H. nui* sp. n. from the south of the country.

DISTRIBUTION: *Heptathela tonkinensis* is known only from the holotype collected in a forest near Khà là (this spelling is given on the laeser-printed label in the tube with the specimen; in the original description the name of the locality is spelled "Kha-lé"), in the valley of the Song (= river) Luc Nam, northeast of Hanoi (Simon, 1909: 69, 71). This locality probably corresponds to the village of Kha Le, about 15 km east of the township of Luc Nam in Bac Giang Province, northern Vietnam.

***Heptathela tomokunii* Ono, 1997**

Figs 39-43

Heptathela tomokunii Ono, 1997a: 24-26, figs 1-8 (description of male and female).

MATERIAL EXAMINED: NSMT-Ar 3396-3398; male holotype (matured 8.X.1995), female "allotype", 1 female paratype; Vietnam, Vinh Phu Province, Tam Dao, 900 m; 15./21.IX.1995; leg. H. Ono.

REMARKS: Diagnosis and description were given by Ono (1997a). The following can be added: cymbial projection only moderately developed, quite wide (Fig. 39); paracymbium short and wide at base, at an acute angle to axis of cymbium (Ono, 1997a: fig. 2), similar to that of *H. tonkinensis*; subtegulum exceptionally long (Fig. 40); contrategulum with denticles on distal edge modified into a series of parallel ribs running down to 1-2 isolated ventral denticles near proximal margin (Figs 39-40); tegulum with quite low, narrowly arched marginal apophysis and with quite short terminal apophysis (Figs 39, 41) carrying a pronounced, strongly bulging dorsal extension with a coarsely dentate edge (Fig. 39; Ono, 1997a: fig. 4) not in contact with edge on marginal apophysis; genital atrium with some hairs on ventral side near posterior and lateral margins (Fig. 42); bursa copulatrix short, anterior margin widely arched; all receptacles simple and smooth [Fig. 43; also confirmed for the "allotype", though the corresponding illustration (Ono, 1997a: fig. 6) indicates indistinctly cauliflower-shaped receptacles], not developed as cauliflower-shaped receptacular clusters as in other Heptathelinae examined; larger lateral pair of receptacles sessile, slightly displaced onto dorsal wall of bursa copulatrix; smaller median pair of receptacles stalked [on common socket in paratype (Fig. 43), on individual stalks in "allotype" (Ono, 1997a: fig. 6)] and slightly displaced onto ventral wall (Fig. 43). "Tibial spurs" present on legs I-III of female, on last exuvia of male and also on mature male (with a few "spurs" reduced).

RELATIONSHIPS: Due to similarities in the palpal organ of males (moderately developed cymbial projection; short, wide paracymbium at an acute angle to the axis of the cymbium; long subtegulum; low, arched marginal tegular apophysis; pronounced dorsal extension of terminal tegular apophysis), *H. tomokunii* appears to be more closely related to *H. tonkinensis* (female unknown) than to *H. australis* and *H. nui* sp. n. More or less pronounced displacements of the lateral pair of receptacles onto the dorsal wall of the bursa copulatrix in *H. tomokunii*, *H. australis* and some *Ryuthela* species are considered homoplastic (see Discussion).

DISTRIBUTION: This species is only known from the type locality, the Tam Dao hill station, about 85 km northwest of Hanoi, in northern Vietnam.

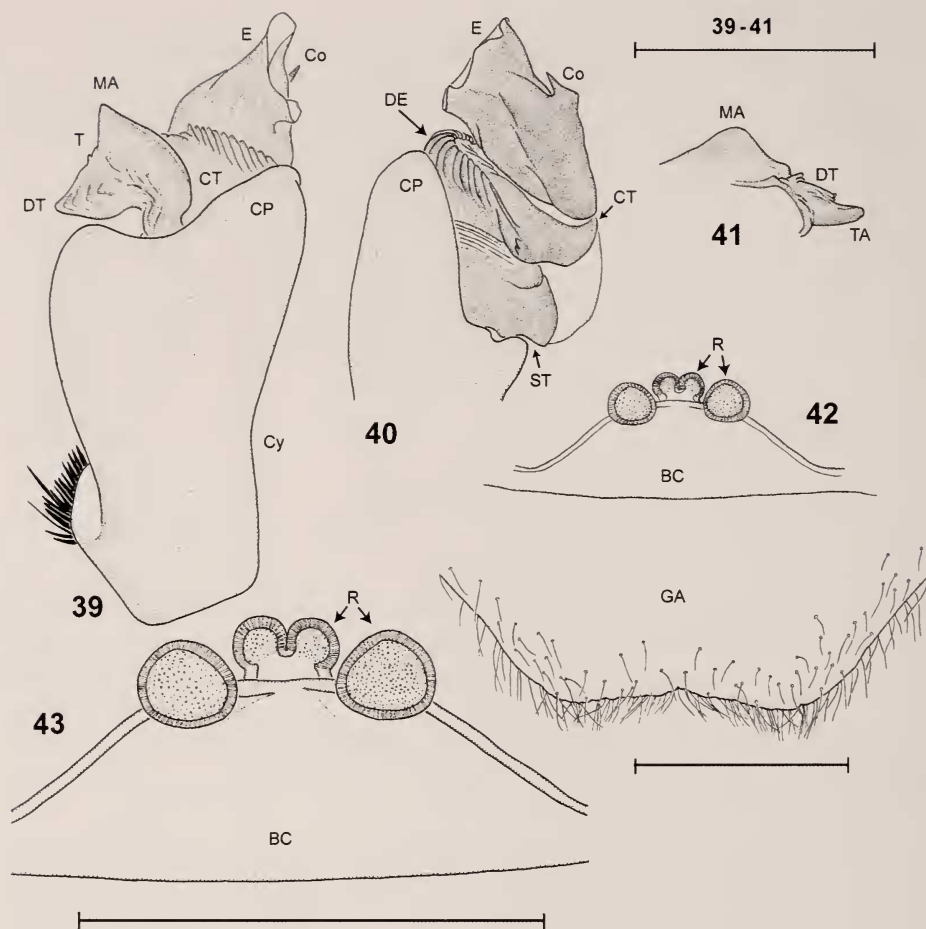
***Heptathela kikuyai* Ono, 1998**

Figs 44-45

Heptathela kikuyai Ono, 1998: 16-19, figs 11-16 (description of male and female).

MATERIAL EXAMINED: NSMT-Ar 8718; 1 male; Japan, Kyushu Island, Oita Prefecture, Hita-shi; 15.X.2006; leg. T. Irie. – NSMT-Ar 3545; 2 females; Kyushu Island, Miyazaki Prefecture, Nishi-ushuki-gun, Takachiho-cho; 8.-14.IX.1996; leg. H. Ono.

DISTRIBUTION: Known from several localities in the northwestern part of Kyushu Island, Japan.



FIGS 39-43

Heptathela tomokunii Ono, 1997, male holotype (39-41) and female paratype (42-43). (39) Distal part of left palp, prolateral view. (40) Left palpal organ, ventral view. (41) Marginal and terminal apophysis of tegulum of left palp, ventral view. (42) Vulva, dorsal view; dorsal and lateral walls of genital atrium not shown. (43) Bursa copulatrix, dorsal view. R=receptacle; other abbreviations as in Figs 1-20. Scale lines 1.0 mm.

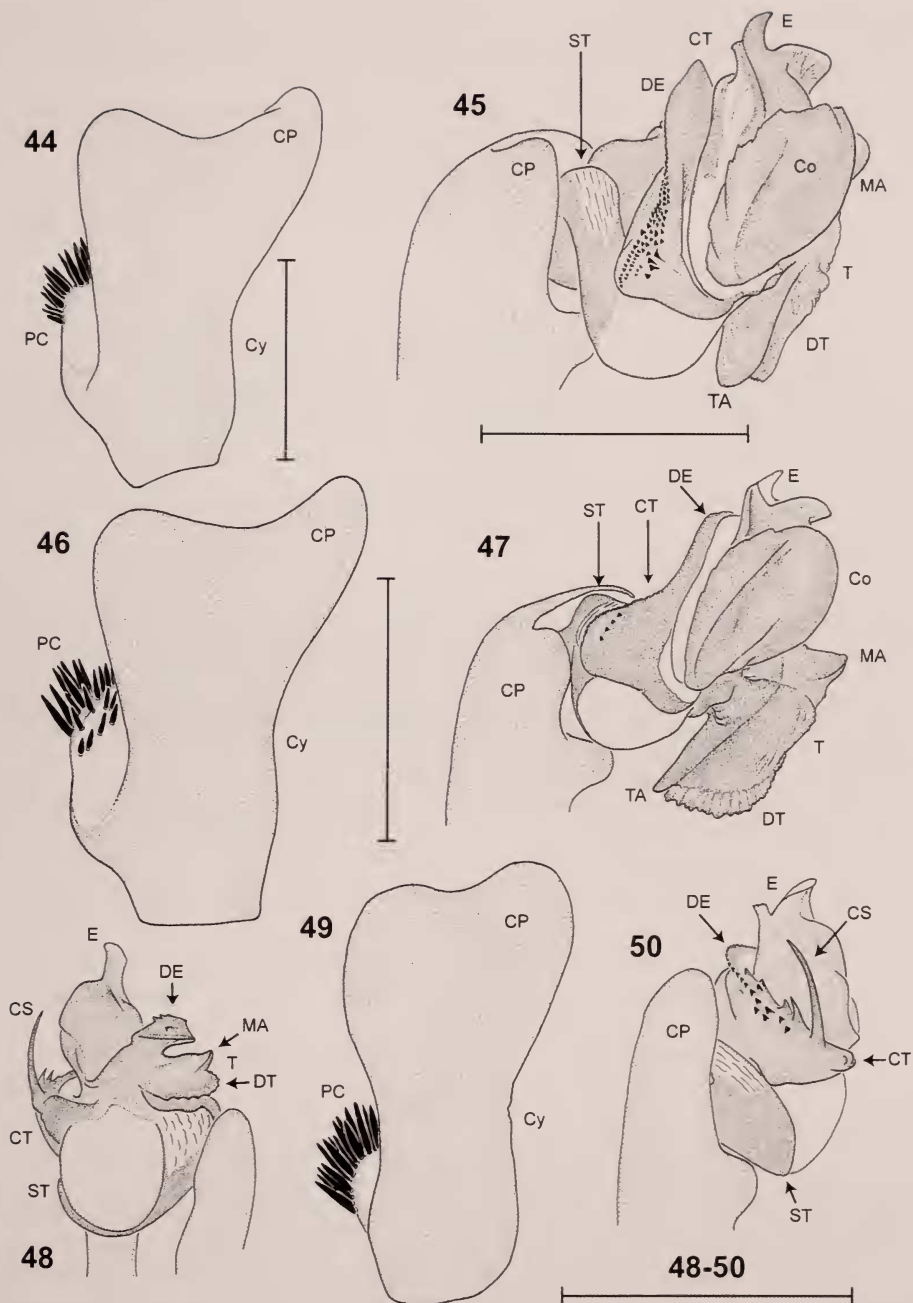
Heptathela kimurai (Kishida, 1920)

Figs 46-47

Liphistius kimurai Kishida, 1920: 362, fig. 1 (description of male and female); type species of *Heptathela*. For a complete synonymy, see Platnick (2011).

MATERIAL EXAMINED: NSMT-Ar 3549; 1 male; Japan, Kyushu Island, Kagoshima-shi; 7.XI.1970; leg. K. Tanaka. – NSMT-Ar 8717; 1 female; Kyushu Island, Kagoshima-shi, Shiroyama; 25.XI.1997; leg. H. Ono.

DISTRIBUTION: Known from several localities in the southern part of Kyushu Island, Japan.



FIGS 44-50

Heptathela kikuyai Ono, 1998, male (44-45); *Heptathela kimurai* (Kishida, 1920), male (46-47); *Ryuthela owadai* Ono, 1997, male holotype (48-50). (44, 46, 49) Left cymbium, prolateral view. (45, 47, 50) Left palpal organ (45 and 47 slightly expanded), ventral view. (48) Same, retrolateral view. CS = contratergular spine; other abbreviations as in Figs 1-15. Scale lines 1.0 mm.

***Ryuthela owadai* Ono, 1997**

Figs 48-50

Ryuthela owadai Ono, 1997b: 155-157, figs 15-18 (description of male).- Ono, 2001: 151-153, figs 1-3 (description of female).

MATERIAL EXAMINED: NSMT-Ar 3459; male holotype; Japan, Okinawa Prefecture, Tokashiki Island, Aharen, about 100 m; 11.X.1990; leg. M. Owada. – NSMT-Ar 8717; 1 female; Okinawa, Tokashiki Island, Tokashiku, 30 m; 17.I.2001; leg. H. Ono.

DISTRIBUTION: Known only from the Tokashikijima Island, Ryukyu Islands, Japan.

***Ryuthela nishihirai* (Haupt, 1979)**

Heptathela nishihirai Haupt, 1979: 356-362, 365, figs 6-13 (description of male and female); type species of *Ryuthela*. For a complete synonymy, see Platnick (2011).

MATERIAL EXAMINED: NSMT-Ar 422-423; 1 male (matured X.1977) and 1 female syntypes; Japan, Shuri, Okinawa, Ryukyu Islands; 15.III.1976; leg. M. Nishihira & J. Haupt. – MHNG (coll. S. Heimer), without registration number; 1 female; Japan, Ryukyu Islands, without further data.

DISTRIBUTION: Known from several localities on Okinawa Island, Japan.

Liphistiinae Thorell, 1869***Liphistius ornatus* Ono & Schwendinger, 1990**

Figs 51-54

Liphistius ornatus Ono & Schwendinger, 1990: 166-170, figs 1-8 (description of male and female).

MATERIAL EXAMINED: MHNG, without registration number; male holotype, 1 male paratype, 4 female paratypes; Thailand, Chanthaburi Province, Khao Soi Dao Wildlife Sanctuary, 300-400 m; 9.V.1987; leg. P. Schwendinger.

DISTRIBUTION: Known only from the type locality in the southern part of eastern Thailand.

***Liphistius thaleri* Schwendinger, 2009**

Figs 59-64

Liphistius thaleri Schwendinger, 2009: 1255-1260, figs 1-12 (description of male and female).

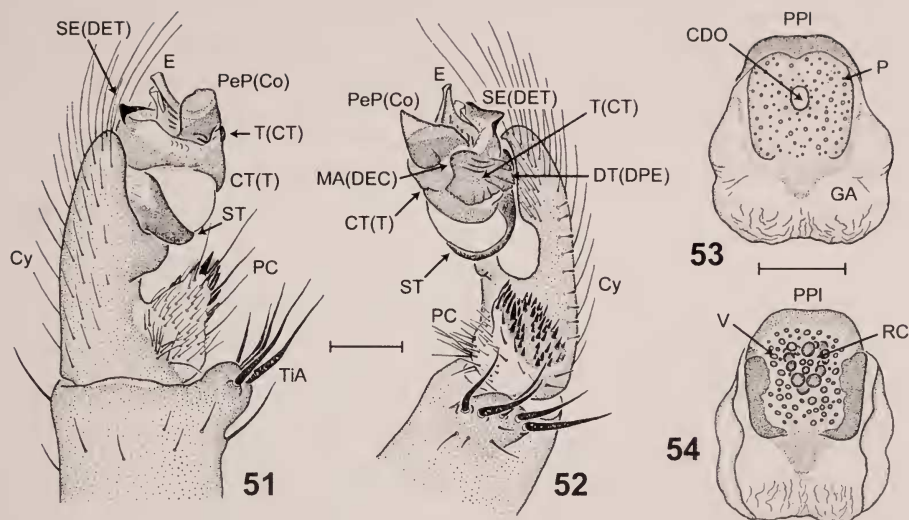
MATERIAL EXAMINED: MHNG, without registration number; male holotype, 5 male paratypes, 8 female paratypes; Thailand, Trang Province, Libong Island, 30 m; 20.VII.2005; leg. P. Schwendinger.

DISTRIBUTION: Known only from Libong Island in southern Thailand.

DISCUSSION

TAXONOMIC CHARACTERS AND TERMINOLOGY: Different and partly contradictory terminology (for a summary see Table 1) for genital structures of liphistiid spiders has been used in taxonomic publications by various authors.

Conductor: Haupt (1979: 358, 360-361, figs 8-10 and subsequent papers of the same author) used the term “conductor” for a distad-directed spine-like structure on the palpal organ of *Ryuthela* males. This spine arises on the ventral side of the contrategulum and is actually a strongly elongate denticle, the last (proximal-most) one in a series (continuous or interrupted) of denticles that run down from the distal edge of the contrategulum in all heptatheline palps examined (denticles indistinctly developed in



Figs 51-54

Liphistius ornatus Ono & Schwendinger, 1990, male holotype (51-52) and female paratype (53-54). (51) Distal part of left palp, ventral view. (52) Same, retrolateral view. (53) Vulva, dorsal view; dorsal and lateral walls of bursa capulatrix and genital atrium not shown. (54) Same, ventral view. CDO = central dorsal opening; Co = conductor; CT = contrategulum; Cy = cymbium; DEC = distal edge of "contrategulum"; DET = dorsodistal edge of "tegulum"; DPE = dentate proximal edge of "contrategulum"; DT = dorsal extension of terminal apophysis of tegulum; E = embolus; GA = genital atrium; MA = marginal apophysis of tegulum; P = medium-sized pore (leading to ampulliform vesicle); PC = paracymbium; PeP = paraembolic plate; PPI = poreplate; RC = receptacular cluster; SE = sharp distal edge of contrategulum; ST = subtegulum; T = tegulum; TiA = tibial apophysis; V = ampulliform vesicle. Scale lines 1.0 mm. Modified from Ono & Schwendinger, 1990: figs 1-4, with permission from the Bulletin of the National Science Museum (Tokyo).

H. kimurai, Fig. 47; modified to ribs in *H. tomokunii*, Figs 39-40). In *R. owadai* the three proximal denticles are elongate to various degrees (Figs 48, 50; Ono, 1997b: figs 16-18). Thus the "conductor" of *Ryuthela* is not fused with the contrategulum as suggested by Haupt (1983: 286; 2003: 71), it is an original part of the contrategulum and as such also of the bulbal sclerite II sensu Kraus (1978: 237, figs 2-4). In other heptatheline genera the conductor is a structure of various shapes that arises from the ventral base of the embolus (or embolus complex) and thus belongs to bulbal sclerite III. Consequently the "conductors" of both groups are not homologous and therefore should not both be called the same. In his descriptions of various *Ryuthela* species Ono correctly notes: "contrategulum with a basal spine; conductor not developed" (e.g., Ono, 1997b). The elongate basal denticle of the contrategulum, in the following called contrategular spine, is unique within the Liphistiidae and a clear synapomorphy for species in *Ryuthela*. Raven (1985: 15, 16) also did not recognize the different origins of the *Ryuthela* and *Heptathela* "conductors" but just their different shapes, and gave this as one of the reasons to synonymise *Ryuthela* with *Heptathela* (*Ryuthela* was later removed from synonymy by Haupt, 2003: 71).

The conductor of *Heptathela* is on the same bulbal sclerite (III) and essentially in the same position as the “paraembolic plate” (also called “scale-like plate of the ventral embolus edge”, “proximal edge of embolus” and “Basalkante des Embolus”) present in many species of *Liphistius* (especially in those of the *trang*-group; Figs 51-52). These sclerites differ only in shape and in distance to the embolus proper: in *Liphistius* the paraembolic plate is wide, short or long, fairly remote from the embolus and slightly inclined from it, whereas in non-*Ryuthela* heptathelines the conductor is wide or narrow, long, usually lies much closer to the embolus and runs more or less parallel to its surface. The relative position of the conductor in *H. tonkinensis* (type species of “*Nanthela*”; Figs 34, 36) is intermediate between that of *Liphistius* and *Heptathela*. Differences in shape [paraembolic plate scale-like (Fig. 51) or only developed as a low wide edge in *Liphistius* (Schwendinger, 1998: fig. 1A-D, I); conductor leaf-shaped in *Heptathela* from Japan (Haupt, 2003: fig. 52F-K, M-P, fig. 62G-L), proximally broad and usually carrying three more or less pronounced, acutely pointed tips in “*Sinothela*” (Haupt, 2003: fig. 52L, fig. 62D-F), blade-like, spiniform and smooth, or spiniform and apically dentate in “*Nanthela*” (Haupt, 2003: fig. 62C)] do not exclude that these structures are homologous. This was stated by Raven (1985: 15) and vigorously refuted by Haupt (2003: 92); we here support Raven’s view.

The terms “conductor” and “contrategulum” were confused in Ono’s (1998) taxonomic treatment of the males of five *Heptathela* species from Kyushu Island (Japan). What is correctly referred to as “conductor” in the descriptive text (except on page 21), is incorrectly called “contrategulum” in the legends to the corresponding figures.

Tegulum: Tegulum and contrategulum are the two more or less distinctly outlined parts of the ring-shaped bulbal sclerite II of the palpal organ in Liphistiidae. In the Heptathelinae the tegulum extends over the dorsal and retrodorsal side of the bulb and carries two apophyses: 1) Dorsally lies the distad-directed marginal apophysis over which runs a sharp distal edge from the prolateral to the retrolateral side. This apophysis is long and pointed in *H. australis* and *H. nui* sp. n. (Figs 2-5, 10, 22-25, 28-29), short and arched in the other heptatheline species examined (Figs 34, 37-38, 39, 45, 47-48). 2) Retrolaterally lies the retrolaterad-directed terminal apophysis over which runs a more or less coarsely dentate (least developed in *R. owadai*) dorsal edge perpendicular to the distal edge on the marginal apophysis. The terminal tegular apophysis is distinctly developed in “*Nanthela*” and *Heptathela* (Figs 3, 5, 10-14, 23, 25, 28, 34, 36-39, 41, 45, 47), indistinctly so in *Ryuthela* (Fig. 48). In *H. australis* and *H. nui* sp. n. the dorsal side of the terminal tegular apophysis is only moderately extended and slightly arched, with the dorsal dentate edge only little elevated (Figs 5, 25), in the other Heptathelinae examined it is strongly protruding into a widely arched extension (Figs 34, 36, 39, 47-48; not visible in Fig. 45). In *H. kikuyai* and *H. kimurai* there is a coarsely dentate third edge on the tegulum (= the “first edge” of Song & Haupt, 1984: 444) which starts at the point where the edges of the marginal and terminal tegular apophyses meet, and from there it runs down the prodorsal side to the base of the tegulum. This edge is not produced into an apophysis as on the other two tegular edges. This condition appears to be characteristic for *H. kimurai* (the type species of *Heptathela*) and its closest relatives. In the other Heptathelinae the edges of the marginal and terminal apophyses do not meet prodorsally and no third edge is present.

In *Liphistius* the tegulum is less obvious, because it seemingly does not possess the same apophyses as the tegulum of the Heptathelinae. The so-called "tegular process" of some *Liphistius* species arises from the opposite (= ventral to proventral) side of bulbal sclerite II and thus belongs to the contrategulum. The contrategular process is probably apomorphic for *Liphistius*, as is also the subtegular apophysis (both present only in some species); both apophyses are absent in all Heptathelinae. What was previously called "tegulum" in *Liphistius* therefore does not correspond to the tegulum in the Heptathelinae. There is, however, a sclerotised area on the retrodorsal side of bulbal sclerite II in *Liphistius* that is connected to the larger part (= the contrategulum) of bulbal sclerite II by a narrow sclerotised area and that carries a sharp distal edge in most species and a dentate marginal or submarginal proximal edge in all species (Fig. 52, Schwendinger, 1996: figs 1, 12, 21, 31, 39, 46, 55, 65, 74, cf. Figs 4, 24). These two edges, though being more two-dimensional, resemble the marginal and terminal tegular apophyses of Heptathelinae and they lie at the same position on the palpal organ. Haupt (1983: figs 1c, 3-4) called the sclerite of the *Liphistius* palp which carries these two edges the "contrategulum", and that appellation was followed in papers on *Liphistius* by Ono and by Schwendinger. We assume that Haupt regarded this sclerite as the "contrategulum" because of a misinterpretation of his own illustration (see Haupt, 1983: fig. 1c) that shows a distinctly expanded male palp of *L. malayanus* Abraham, 1923 in which the so-called "contrategulum (K)" was rotated to the ventral side where the contrategulum is situated in the Heptathelinae (see Haupt, 1983: fig. 1b). In his illustrations of non-expanded *Liphistius* palps (see Haupt, 1983: figs 3b-c, 4a-b), however, the so-called "contrategulum (K)" lies on the other side, retrodorsally, where the tegulum of the Heptathelinae is situated. Correspondingly the latter figures show the so-called "tegulum (T)" proventrally, where the Heptathelinae have the contrategulum. Haupt has obviously confused these terms in both taxa. The tegulum of *Liphistius* (hitherto incorrectly called "contrategulum") is much shorter and narrower than that of the Heptathelinae, and it is confined to the retrodorsal side of bulbal sclerite II. The dentate proximal or subproximal edge of the tegulum of *Liphistius* is presumably homologous with the dentate edge on the dorsal side (protruded into a dorsal extension in some species) of the terminal tegular apophysis of the Heptathelinae, and the more or less distinctly developed distal edge of the *Liphistius* tegulum is presumably homologous with the marginal apophysis of the Heptathelinae (Fig. 52 cf. Figs 4, 24). A fairly simple tegulum (more reduced than in *Heptathela* but less than in *Liphistius*) is also present in *Ryuthela owadai* (Fig. 48). We consider the small tegula of *Liphistius* and *Ryuthela* as homoplastic reductions, which implies that the palpal organs of *Liphistius* and (to a lesser degree) *Ryuthela* are more derived than those of *Heptathela*.

Contrategulum: Haupt (1983: 277) introduced the term "contrategulum" for the prolateral to ventral part of bulbal sclerite II that opposes the tegulum. In the Heptathelinae tegulum and contrategulum are more or less distinctly separated by a wide membranous zone (haematodocha) retroventrally, thus forming a broken ring. Prodorsally, however, both parts are widely fused and it is difficult to tell where the contrategulum ends and the tegulum begins. An indicator is the sharp distal edge of the contrategulum portion which more or less abruptly ends prolaterally in *H. australis*

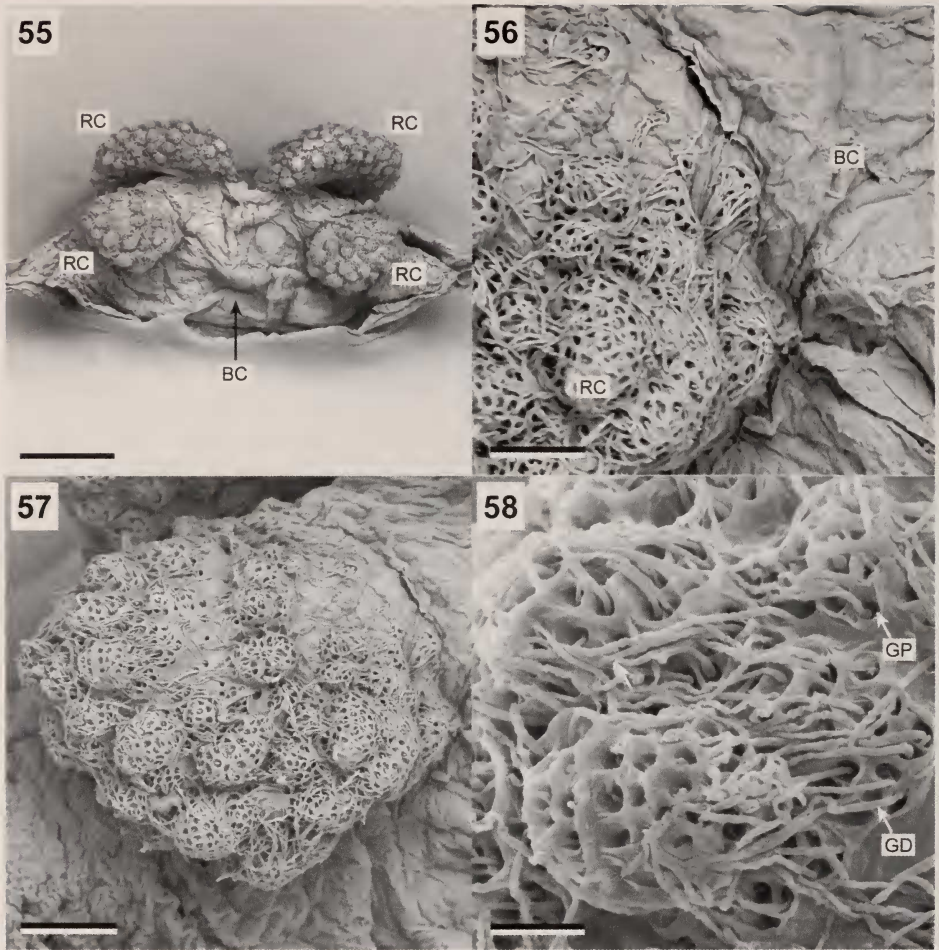
(Fig. 2), *H. nui* sp. n. (Fig. 22), *H. kikuyai* and *H. kimurai*, whereas in *H. tonkinensis* (Figs 34, 36), *H. tomokunii* (Fig. 39) and *R. owadai* (Fig. 48) it fades out between the marginal tegular apophysis and the embolus. More proximally at that place contrategulum and tegulum are usually fused with each other without a transition, though in *Heptathela* males from Japan examined a small invagination in the proximal margin of bulbal sclerite II presumably marks the border between both parts. In *Ryuthela* this pattern is modified and the distinction between contrategulum and tegulum is more visible on the dorsal side of the palpal organ: the contrategulum is much wider than in other heptathelines (as wide as in *Liphistius*) and extends distally past the tegulum to the retrolateral side in an almost complete circle; a deep, almost horizontal furrow divides both sclerites dorsally (Fig. 48), and only on the ventral side are tegulum and contrategulum completely fused (Fig. 50). In *R. nishihirai* tegulum and contrategulum appear to be completely separated (see Haupt, 1979: 360, fig. 9). In *Liphistius* the contrategulum is much more extensive than the tegulum, almost completely embracing the middle portion of the palpal organ (as also in *Ryuthela*, but there the tegulum is much wider than in *Liphistius* and overlaps the contrategulum). Retrolaterally the large contrategulum and the much smaller tegulum are connected by sclerotised bridges (the more dorsal one always narrower than the more ventral one) and form a closed ring (Fig. 52). What was previously called "tegular process", "distal edge of tegulum" and "dorsal edge of tegulum" in various publications on *Liphistius* by Haupt and by Schwendinger, are in fact parts of the contrategulum.

In Heptathelinae the contrategulum usually carries on its distal edge (which is divided into a sharp outer edge and a dentate inner edge in *H. australis* and *H. nui* sp. n.) a row of denticles which are more or less distinctly connected to a few (in some species isolated) denticles ventro-proximally. These denticles were subject to evolutionary modifications of taxonomic significance. In several species they have multiplied and become more than one row deep: in *H. nui* sp. n. two rows proximally (Fig. 23), in *R. owadai* three rows proximally (Fig. 50), in *H. kikuyai* several rows proximally (Fig. 45) and in *H. tonkinensis* several irregular rows on most of its distal edge (Fig. 36); in *H. tomokunii* (Figs 39-40) and seemingly also in *H. hongkong* Song & Wu, 1997 (Haupt, 2003: fig. 51D) they have transformed into a series of parallel edges or ribs. Such ribs are also present in some *Liphistius* species where they are probably homoplastic (see Schwendinger, 1995: figs 22-23, 26-27; Schwendinger, 1996: figs 12, 15-17; Schwendinger, 1998: fig. 5b, e-f). In *Ryuthela* spp. the basalmost of these denticles (in *R. owadai* to a lesser degree also two adjacent ones; Figs 48, 50) has become strongly elongate and spine-like. This modified contrategular denticle of *Ryuthela* is clearly not homologous to the conductor (or paraembolic plate) of other Liphistiidae (see discussion of conductor), but it presents a clear synapomorphy for species in *Ryuthela*.

Cymbial projection: Haupt (2003: 69, 94, character 23 in table 11 and fig. 61) considers the elongate proventral cymbial lobe as "autapomorphic" (Haupt, 2003: 94; it should read "synapomorphic") and distinctive for males of species in the genus "*Nanthela*". However, this modification is also present in two *Heptathela* species from Japan examined: *H. kikuyai* (Fig. 44) and *H. kimurai* (Fig. 46; the type species), and it is also discernible in Song & Haupt's (1984: fig. 1c) illustration of the male palp of

H. schensiensis (previously in "*Songthela*") and in Haupt's (1983: fig. 10a-d) illustrations of the male palp of *Ryuthela nishihirai* and *R. ishigakiensis* Haupt, 1983. In *R. owadai* the cymbial projection is only weakly developed (Fig. 49). In some *Liphistius* species (e.g., *L. bristowei* Platnick & Sedgwick, 1984 and *L. batuensis* Abraham, 1923; in MHNG examined), on the other hand, it is the prodorsal cymbial lobe (instead of the proventral one) that is moderately elongate. Thus it appears that one of the cymbial lobes (the proventral one in Heptathelinae, the prodorsal one in *Liphistius*) has become elongated to various degrees independently in different phylogenetic lineages. The taxonomic value of this character at the generic level has thus been overestimated.

Vulva: HEPTATHELINAE. The vulva of heptatheline spiders is composed of two main parts (see Fig. 19): 1) The posterior part is a long and wide entrance area (= the genital atrium) furnished with numerous hairs on the dorsal and ventral walls in *H. australis* (Fig. 16), *H. nui* sp. n. (Fig. 31) and *H. tomokunii* (Fig. 42), but only on the dorsal wall in *H. kikuyai*, *H. kimurai*, *R. owadai* and *R. nishihirai*. The genital atrium is overlapped by a more or less tongue-shaped projection of the posteromedian margin of the genital sternite. 2) The anterior part of the vulva is a blind-ending pouch (= the bursa copulatrix) in the form of a flattened bell (see Ono, 2002a: fig. 3), plano-convex or trapezoidal in dorsal and ventral view, with walls consisting of a light yellow, tough, leathery but not sclerotised cuticle (Figs 16-19, 31-33, 42-43, 55). As already stated by Forster (1980: 280), there is no sclerotised structure in the vulva of heptatheline spiders that can be called a genital plate (an incorrect term used by several authors; see Table 1]. Usually no pores are present in the walls of the bursa copulatrix (Figs 55-56), but the largest *H. australis* female has tiny pores on the small vesicles that lie scattered between the receptacular clusters (Fig. 16). This could be an atavism (see *Evolution of female copulatory organs*). From the dorsal side of the vulva, where both main parts meet at an obtuse angle, a short and wide, dorsoventrally depressed membranous collar (= the uterus externus) leads dorsad to the mesodermal part of the oviduct (= the uterus internus) and further to the ovary (Fig. 19). In the illustrations by Haupt (1983: fig. 2b) the entrance to the uterus externus is erroneously shown at the anterior end of the bursa copulatrix, which is in fact a cul-de-sac. The anterior margin of the bursa copulatrix carries between one and four sessile or stalked, mostly cauliflower-shaped protuberances (= the receptacular clusters) composed of numerous more or less strongly sclerotised vesicles (= the receptacles). The composite structure of the receptacular clusters in heptathelines (for *Ryuthela nishihirai*) was first recognized by Haupt (1979: 365). The walls of these vesicles are perforated by tiny micropores through which surrounding glands empty. The proximal, cuticular portions of the gland ducts that are sticking out of the micropores like fine hairs (Figs 56-58; SEM-micrographs taken from exuviae) clearly show that these are indeed gland pores. In the two females of *H. tomokunii* examined these anterior protuberances on the bursa copulatrix are simple in shape and have a fairly smooth surface (though also perforated by micropores; Figs 42-43) and may be called receptacles. This indicates a trend towards simplification, which is also seen in the receptacular clusters of some *Liphistius* species that have become smooth and digitiform (Sedgwick & Schwendinger, 1990; fig. 6; Schwendinger, 1996: figs 18-20, 52-54). In *H. australis* and other species previously



FIGS 55-58

Heptathela australis (Ono, 2002), SEM-micrographs of genitalia from the exuvia of one female, dorsal views. (55) Entire bursa copulatrix with receptacular clusters. (56) Border between dorsal wall of bursa copulatrix (without pores) and lower left receptacular cluster (with gland pores). (57) Lower left receptacular cluster. (58) Detail of the same showing gland pores and cuticular parts of gland ducts. BC = bursa copulatrix; GD = cuticular (proximal) part of gland duct; GP = gland pore (micropore); RC = receptacular cluster. Scale lines: 14 μ m (58), 31 μ m (56), 56 μ m (57), 236 μ m (55).

placed in “*Songthela*” by Ono (2000), two of these receptacular clusters (the lateral ones) have become displaced onto the dorsal wall of the bursa copulatrix and are directed dorsad instead of anteriad (Figs 16-19, 55).

Illustrations in the original description of *H. goulouensis* Yin, 2001 show a very different type of vulva (without a bursa copulatrix but instead with a pair of bifid “curved, tube-like stalks”, each carrying a median and a lateral receptacle or receptacular cluster; Yin, 2001: figs 5-6, 8-9) which is similar to the vulvae of certain mygalomorph spiders. If correct, this would be most unusual for liphistiid spiders. A

re-examination of these specimens may show that the true boundaries of the bursa copulatrix were not recognized and that the “stalks” are actually zones of different pigmentation, or a mass of sperm inside the bursa copulatrix. Similar “stalks” and a short bursa copulatrix were illustrated for the holotype of *H. sapana* (Ono, 2010: fig. 16). The so called “didymous phenomenon” displayed by the female paratype of *H. goulouensis* (Yin, 2001: figs 8-9) is most likely based on a spider that was preserved prior to moulting, which has the new cuticle of the vulva already formed underneath the old cuticle.

The number of receptacles or receptacular clusters and their position on the bursa copulatrix is variable and this has been used to recognize groups of species which were given generic rank. *Ryuthela* is characterized by only two anterior receptacular clusters situated close to each other (Haupt, 2003: 71, fig. 53), but a rudimentary pair of additional (lateral) receptacular clusters is still present in the female “allotype” of *R. owadai* (see Ono, 2001: figs 2-3). This is not so in the corresponding female paratype examined. Non-*Ryuthela* Heptathelinae usually have four more or less distinctly developed receptacles or receptacular clusters, but distinction from *Ryuthela* is not clear-cut. Lateral receptacular clusters have become more or less fused with median ones in several *Heptathela* species (see Ono, 1998: figs 9-10, 15-16, 17-20, 31-32; Haupt, 2003: fig. 54), resulting in only two anteromedian receptacular clusters which are generally more widely separated from each other than in *Ryuthela*. The holotypes of *H. hunanensis* Song & Haupt, 1984 and of *H. cucphuongensis* have the median pair fused and the lateral pair still isolated, resulting in a vulva with three anteromedian receptacular clusters (Song & Haupt, 1984: fig. 3e; Ono, 1999: fig. 8). Ono (2000) used this intermediate character state to establish the genus “*Vinathela*” (misspelled “*Viathela*” and placed in the synonymy of *Heptathela* by Haupt, 2003: 71, 79). Fusion of receptacular clusters has gone even further: the illustrated vulva of *R. iheyana* Ono, 2002 has a single, wide and short anteromedian receptacular cluster (Ono, 2002b: figs 2-3); the holotype and one female paratype of *R. sasakii* Ono, 1997 have a single, long and narrow anteromedian receptacular cluster (Ono, 1997b: figs 5-8). We consider all these forms as intermediate stages of reduction and fusion of the four anterior receptacular clusters that are plesiomorphically present in heptatheline spiders. Such modifications probably have evolved independently in different phylogenetic lineages and should be treated with caution when establishing relationships between species.

Two receptacular clusters displaced to the dorsal side of the bursa copulatrix (Figs 16-19, 55) is another kind of modification in heptatheline vulvae. This character state was used by Ono (2000) to establish the genus “*Songthela*”, but as *H. australis* (described in “*Songthela*”) has it and the obviously closely related *H. nui* sp. n. not, it can no longer be used as distinctive on the generic level. All the more so because several transitional steps exist: the lateral receptacular clusters of *H. tomokunii* (see Figs 42-43; Ono, 1997a: fig. 6), *H. sinensis*, *H. schensiensis* (see Song & Haupt, 1984: fig. 3a-b, f) [the latter two placed in “*Abcathela*” by Ono, 2000, in “*Sinothela*” by Haupt, 2003 and then in “*Songthela*” by Platnick, in an earlier version of his 2011 online catalogue] and of *H. yunnanensis* Song & Haupt, 1984 (see Song & Haupt, 1984: fig. 3f) are also slightly displaced onto the dorsal wall of the bursa copulatrix, but not as far back as in *H. australis* (Figs 16-18, 55) and as in *H. hangzhouensis* (see Song &

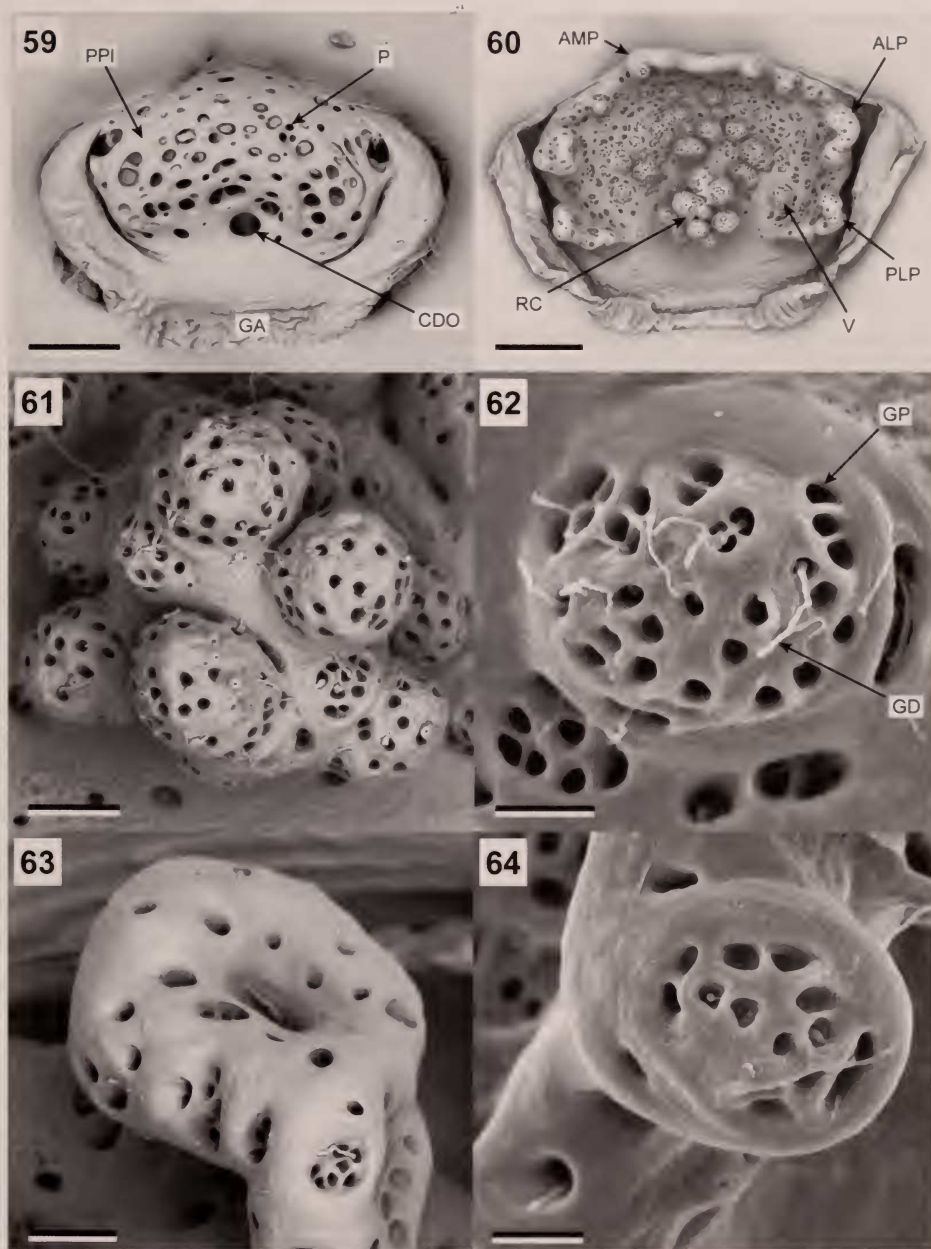
Haupt, 1984: fig. 3c-d) (both species previously in "*Songthela*"). The median pair of receptacles (reduced receptacular clusters) of *H. tomokunii* (Figs 42-43; in addition to the lateral pair which was slightly displaced onto the dorsal wall) and of some *Ryuthela* species (see e.g., Ono, 1997b: figs 5-14, 19-22) is even sitting slightly below the anterior margin of the bursa copulatrix, on its ventral wall (thus on the same side as the receptacular cluster of *Liphistius*).

LIPHISTIIDAE. The heptatheline vulva is largely different from the vulva of *Liphistius* which carries no anterior receptacular clusters. In that genus the dorsal wall of the bursa copulatrix is a thin transparent membrane that never carries any modifications apart from a pigmented spot opposing the macropore in the ventral wall in a few large females. (In *Liphistius* the entrance to the uterus externus is also situated at the border between atrium and bursa copulatrix, not at the anterior end of the bursa copulatrix as shown in Haupt, 1983: fig. 2a). The ventral wall of the bursa copulatrix in *Liphistius* is strongly sclerotised and includes a true genital plate (= the poreplate) perforated dorsally by medium-sized pores that lead inside small ampulliform vesicles on the ventral side (Figs 53-54, 59-60). The appellation "gland pores" used in a paper by Schwendinger (1996) for these vesicles is incorrect; the gland pores (= micropores) are actually on the outside of the vesicles (ventrally on the poreplate), as clearly visible in SEM-micrographs by Kraus (1978: fig. 8; see also Fig. 62). Kraus (1978: 242-243, figs 6-8) called these vesicles "circular structures [or circular areas] ... interpreted ... as a pore system for glands ... [which] must not be confused with the receptacula". Kraus (1978: fig. 8) first showed SEM-micrographs of micropores in *Liphistius* and recognized the function of the ampulliform vesicles, but the corresponding lettering is misleading [in fig. 8 the ventral surface of a vesicle is labelled as "gland pore", in fig. 6 the opening (= medium-sized pore) of a vesicle on the dorsal side of the poreplate]. Sperm that enters into the ampulliform vesicles from the dorsal side of the poreplate is thus supplied with (or flushed out by) a secretion of the receptacular glands from the other side. Thus the vesicles on the ventral side of the *Liphistius* poreplate are sperm receptacles.

On the dorsal side of the *Liphistius* poreplate a fairly large central opening (or macropore; CDO in Figs 53, 59) leads to an unpaired, strongly sclerotised receptacle or (in most species) receptacular cluster (Figs 54, 60-61; Haupt, 2003: 68 called this an "unpaired ventral sac") on the ventral side of the poreplate. The central receptacular cluster is perforated by gland pores, and it varies in shape from simple and digitiform (in that case called a receptacle, see Sedgwick & Schwendinger, 1990; fig. 6; Schwendinger, 1996: figs 18-20, 52-54) to complex and cauliflower- or popcorn-shaped (Kraus, 1978: figs 5-8; Platnick & Sedgwick, 1984: figs 69, 80, 87). In the heptatheline vulva no receptacle or receptacular cluster is found at this position (although shown there in Haupt, 1983: fig. 2b), but a slight displacement of the median pair onto the ventral side of the bursal copulatrix can be seen in *H. tomokunii* (Figs

FIGS 59-64

Liphistius thaleri Schwendinger, 2009, SEM-micrographs of vulvae from the exuviae of three female paratypes. (59) Ventral wall of opened bursa copulatrix and genital atrium, dorsal view. (60) Same, ventral view. (61) Receptacular cluster. (62) Ampulliform vesicle. (63) Anterolateral



protuberance on rim of poreplate. (64) Posterolateral protuberance on rim of poreplate. ALP = anterolateral protuberance on rim of poreplate; AMP = anteromedian protuberance on rim of poreplate; CDO = central dorsal opening (macropore) to receptacular cluster on other side; GA = genital atrium; GD = cuticular (proximal) part of gland duct; GP = gland pore (micropore); P = medium-sized pore (leading to ampulliform vesicle); PLP = posterolateral protuberance on rim of poreplate; PPI = poreplate; RC = receptacular cluster; V = ampulliform vesicle. Scale lines: 14 μ m (64), 16 μ m (62), 32 μ m (63), 35 μ m (61), 195 μ m (59), 205 μ m (60).

42-43) and in several *Ryuthela* species (Ono, 1997b: figs 9-14, 19-22). In *R. sasakii* this pair has become fused, it possesses a common unpaired, slightly ventrally situated, fairly large opening (macropore; see Ono, 1997b: figs 5, 7), and thus resembles the receptacular cluster in *Liphistius*.

Several *Liphistius* species possess 1-3 pairs of ventrad-directed protuberances on the thickened anterior and lateral margins of the poreplate (Fig. 60). These appear to be synapomorphic for members of superspecies D of the *trang*-group (co-occurring with a synapomorphic subtegular apophysis in males of these species, see Schwendinger, 2009; subtegular apophyses in the *bristowei*-group are homoplastic), but also occur in distantly related species in other species groups (e.g., Platnick & Sedgwick, 1984: figs 13, 21, 78; Schwendinger, 1990: figs 2-4, 37-39, 43-45, 47-49, 53-56). These protuberances are hollow, in contact with the bursa copulatrix through medium-sized pores on the dorsal side of the poreplate, and their walls are perforated with micropores through which gland ducts enter (Figs 60, 63-64). Therefore the ventral marginal protuberances are functional sperm receptacles. Function and position of these protuberances suggest that they are homologous with the receptacular clusters of the heptatheline vulva, but considering that the poreplate in *Liphistius* itself is an apomorphic structure, that is quite unlikely. We regard these protuberances as outgrowths on the thickened margin of the poreplate, which have developed several times independently in *Liphistius*. They are useful for species distinction, and their number and position on the poreplate allow recognizing relationships between species.

Micropores are not only found in the elevated parts of the ventral side of the poreplate, but also in the flat parts between them (Figs 60, 62). Most of the pores there are grouped and sitting in shallow depressions, with membranous gland duct bases sticking out of them, and these groups of sessile micropores are in contact with medium-sized pores on the dorsal side of the poreplate. Thus essentially the whole of the poreplate serves as a sperm receptacle.

Evolution of female copulatory organs: The fact that two very different types of vulvae exist within the Liphistiidae raises the questions: how did they evolve and which one is more derived than the other? Five hypotheses were put forward in an attempt to explain the evolution of female copulatory organs in Liphistiidae and in Araneae as a whole:

1) Platnick & Gertsch (1976: 6), and subsequently Platnick (1977: 13), postulated that in ancestral spiders the palps were pressed simultaneously into the female genital tract during copulation, and that the tips of embolus and conductor of each palpal organ left imprints in the wall of the vulva which developed into receptacles. A vulva with four receptacles, as found in most Heptathelinae and in some basal Mygalomorphae and basal Araneomorphae, is thus plesiomorphic for the Araneae.

2) An alternative hypothesis, put forward by Forster (1980: 277, fig. 12) and further elaborated by Forster, Platnick & Gray (1987: 94-98), presents an archetypical spider vulva with only a large and simple bursa copulatrix supported by a secretory gland system that empties through pores in the anterior wall of the bursa. According to this hypothesis, numerous receptacles (vesicles) developed later by invagination (better called exsacculation) of the bursal wall where the gland pores are situated. In this view the *Liphistius* vulva is relatively primitive because it still has numerous indi-

TABLE 1. Different terminology used for homologous genital characters in three groups of liphistiid spiders by various authors in 14 selected publications. Forster (1980¹); Haupt (1979², 1983³, 2003⁴); Kraus (1978⁵); Ono (1997b⁶); Ono (1998⁷); Ono & Nishikawa (1989⁸); Schwendinger (1990⁹, 1996¹⁰, 2009¹¹), Song & Haupt (1984¹²), Yin (2001¹³), present paper¹⁴. Abbreviations (in parentheses) correspond to those given in Figs 1-64. Terms between inverted commas are considered as inappropriate or incorrect.

<i>Heptathela</i> (see Figs 1-47, 55-58, 67-68)	<i>Ryuthela</i> (see Figs 48-50)	<i>Liphistius</i> (see Figs 51-54, 59-64)
conductor (Co) ^{2, 3, 4, 7, 12, 14} , "contrategulum" (CT) ⁷	-	para-embolic plate (PP) ^{10, 11, 14} ; "posterior" edge of embolus ⁹ ; scale-like proximal embolus edge ⁹ ; broad lamella at base of embolus ^{4, 5} ; Chitinplatte auf Basalkante des Embolus ³ ; conductor ¹⁴
ventro-proximal denticles on contrategulum ¹⁴	"conductor" ^{2, 3, 4} ; spine on contrategulum ⁶ ; contrategular spine (CS) ¹⁴	-
contrategulum (CT) ^{3, 4, 7, 8} , 12, 14	Medianapophyse ² ; contrategulum (CT) ^{6, 14}	"tegulum" (T) ^{3, 4, 9, 10, 11} ; contrategulum (CT) ¹⁴
tegulum (T) ^{3, 4, 7, 8, 12, 14}	tegulum (T) ^{2, 3, 4, 6, 14}	"contrategulum" (CT) ^{3, 4, 10, 11} ; tegulum (T) ¹⁴
terminal apophysis of tegulum ¹² ; third tegular edge ¹² ; dentate edge of dorsal extension of terminal apophysis of tegulum (DT) ¹⁴	dentate edge of dorsal extension of terminal apophysis of tegulum (DT) ¹⁴	dentate proximal edge of "contrategulum" (DPE) ¹⁰ ; "ventral" edge of "contra- tegulum" ¹¹ ; dentate edge of dorsal extension of terminal apophysis of tegulum (DT) ¹⁴
marginal apophysis of tegulum (MA) ^{12, 14} ; second tegular edge ¹²	marginal apophysis of tegulum (MA) ¹⁴	distal edge of "contra- tegulum" (DEC) ¹⁰ ; "dorsal" edge of "contrategulum" ¹¹ ; distal edge of tegulum ¹⁴ ; marginal apophysis of tegulum (MA) ¹⁴
genital plate ^{4, 12, 13} ; Genital- platte ³ ; dorsal and ventral walls of bursa copulatrix ¹⁴	Genitalplatte ³ ; Atrialplatte ³ ; dorsal and ventral walls of bursa copulatrix ¹⁴	Genitalplatte ³ ; Atrialplatte ³ ; receptaculum ⁴ ; chitinous plate ⁵ ; inner plate ⁵ ; internal plate ⁵ ; poreplate (PPI) ^{1, 14}
receptacula ^{1, 3, 4, 12, 13} ; receptacles (R) ¹⁴ ; receptacula organ ¹³ ; receptacular clusters (RC) ¹⁴ ; spermathecae ^{7, 8}	receptacula ^{2, 3, 4} ; receptacular clusters (RC) ¹⁴ ; spermathecae ⁶	receptaculum ^{9, 10, 14} ; receptacular system ⁵ ; central receptacular cluster (RC) ^{9, 10} , 11, 14; pseudo-receptaculum ¹ ; unpaired ventral sac ⁴

vidual receptacles [plus an autapomorphic unpaired "pseudo-receptaculum" (= the central receptacular cluster)] embedded in the poreplate, whereas the heptatheline vulva has developed further away from the ancestral form through a bilateral aggregation of receptacles into receptacular clusters and through a reduction of the poreplate (Forster, Platnick & Gray, 1987: 98).

3) A similar interpretation was given by Kraus (1978: 235, 249), who considers the *Liphistius*-type vulva (with an unpaired central receptacular cluster) as the most primitive within the Araneae and postulated that vulvae with paired receptacles (and also those with unpaired ones) derived from it.

4) Haupt took elements of the previous hypotheses to explain the evolution of female copulatory organs in spiders. He postulated an ancestral vulva with a large bursa copulatrix and irregularly arranged gland pores (Haupt, 1983: 288), as did Forster (1980), but referred to Kraus (1978) who proposed a different hypothesis (see above). Localised receptacles were assumed to have formed later in co-evolution with the split tips of the embolus (Haupt, 1983: 288). In his cladogram of mesothelid systematics and in the corresponding character evaluation Haupt (1990: 136, fig. 1) follows Kraus (1978) and regards the vulva of *Liphistius* as plesiomorphic and that of *Heptathelinae* as apomorphic. Later, however, he noted that "it cannot be decided with certainty whether unpaired or paired receptacula in mesothelid spiders have to be considered as apomorphic for the group" (Haupt, 2003: 93).

5) Raven (1985: 15-16) regarded the vulva of *Ryuthela* (with a single pair of anteromedian receptacles) as plesiomorphic and assumed that the vulvae of *Heptathela* and *Liphistius* derived from it.

In view of the evolutionary tendencies for fusion and posteriad-displacement (to the dorsal and ventral walls) of four anterior receptacles or receptacular clusters in different lineages of heptatheline spiders, we believe that the same has also happened during the evolution of *Liphistius* species. We thus favour a combination of hypotheses 1 and 2 and consider the *Liphistius* vulva as derived from a proto-*Heptathela* vulva. That presumably resembled the vulvae of *H. nui* sp. n. (Figs 31-33) and of species from China and Vietnam previously placed in the genus "*Abcathela*" by Ono (2000), but had a much larger bursa copulatrix carrying four receptacular clusters on its anterior margin and possibly also scattered micro-receptacles on the walls of the bursa copulatrix more posteriorly. Such isolated micro-receptacles (vesicles penetrated by gland pores) are still present in the anterior part of the dorsal surface of the bursa copulatrix of the largest *H. australis* female examined (Fig. 16). This possibly is an atavism.

The pronounced differences in the vulvae of *Liphistius* and *Heptathela* indicate that the separation of both genera goes back much further in time than the separation of *Heptathela* and *Ryuthela*. The vulva of the latter is essentially a *Heptathela* vulva with a strongly reduced bursa copulatrix, with the receptacular clusters of each side fused to one another resulting in a single pair.

This interpretation is in line with the hypothesis of Schwendinger (2009: 1265-1266) that the Mesothelae originated in Euramerica before its integration into Pangaea, and from Euramerica spread eastward onto terranes that successively accreted to eastern Laurasia. In such a scenario, and knowing the very limited powers of dispersal of extant mesothelid spiders, one would rather expect to find the more basal extant species in southern and eastern China than further south, in Myanmar, Thailand, peninsular Malaysia and Sumatra. The latter lands mostly lie on the Sibumasu terrane which accreted to Laurasia later than the Chinese terranes and thus was colonized by Laurasian species later. This zoogeographic hypothesis and its implications for liphistiid phylogeny will be falsified as soon as an early (Palaeozoic or Mesozoic) mesothelid fossil is discovered on land of Gondwanan origin.

"*Tibial spurs*": The function of these paired structures distally on leg tibiae I-III (Platnick & Goloboff, 1985: figs 1-2; Haupt, 2003: fig. 16B-D), which must not be confused with coupling spurs ventrally or prolaterally on tibia I or tibia II in males of many mygalomorph spiders, is not yet understood. Platnick & Goloboff (1985) consider them as part of proprioceptive sense organs in which the "tibial spurs" press against smooth oval patches at the bases of metatarsi I-III (Platnick & Goloboff, 1985: figs 3-4; Haupt, 2003: fig. 16B, D). Haupt (2003: 22, 95, fig. 16), however, assumes that the "tibial spurs", situated close to lyriform organs, are more likely used to monitor hemolymph pressure and strains in the cuticle, because they are allegedly not in contact with the metatarsal patches ("the bristle has no contact to the circular area of thinner cuticle"). This statement is incorrect. On alcohol-preserved specimens with stretched legs, or on a dry, stub-mounted and sputter-coated leg as shown by Haupt (2003: 16D), these structures are usually not in contact with each other, but they are so on live spiders sitting in ambush with slightly bent legs at the burrow entrance. Whatever the function of this sensory system is, its phylogenetic significance as a clear apomorphy of the Liphistiidae is undisputed. We found it to be present in all juvenile (also exuvia of penultimate males) and female liphistiids ever examined by both of us. "Tibial spurs" (but not always the light smooth paired patches on metatarsi I-III) are usually absent in mature males. In the male holotype of *H. tomokunii* and in the male paratype of *L. ornatus* (Ono & Schwendinger, 1990: 169-170) some "tibial spurs" are present but probably no longer functional.

SYSTEMATICS: Discoveries of new species or of the missing sex of described species occasionally challenge the concepts of established supraspecific taxa. This is also the case in the two *Heptathela* species from southern Vietnam. The female of *H. australis* corresponds perfectly to Ono's (2000: 150, fig. 4D) concept of "*Songthela*", where this species was originally placed. Its newly discovered male, however, possesses the two characters considered by Haupt (2003: 69) as diagnostic for "*Nanthela*" (a cymbial projection present, conductor slender and much of its base fused to the embolus), and it also has a character considered in the same paper, on the same page, as diagnostic for *Heptathela* [paracymbium almost as long as cymbium (though relatively shorter in relation to the cymbium of *Heptathela* from Japan because that usually has no pronounced cymbial projection)]. The same type of male palp is present in the closely related *H. nui* sp. n., the female of which, however, possesses a vulva as in species previously placed in "*Abcathela*" (see Ono, 2000: 149-150, fig. 4C). This suggests that three of these four nominal genera ("*Abcathela*", *Heptathela*, "*Nanthela*", "*Songthela*") do not reflect phylogenetic relationships. We rule out that *H. australis* and *H. nui* sp. n. are only distantly related. Geographical proximity and strong overall resemblance of the male palps show that these species are the most closely related. They share four likely synapomorphies in their male palps: 1) a very pronounced cymbial projection (more than in other heptathelines); 2) a long and pointed marginal tegular apophysis; 3) two parallel distal edges (one sharp, the other dentate) on the contrategulum; 4) an unpigmented and unsclerotised distoventral zone on the cymbium. Consequently these two species cannot be kept in different genera, and at the moment it appears most suitable to place them in the genus *Heptathela*.

The generic concept of "*Songthela*" is firmly rejected because the species included clearly do not represent a monophyletic group. Its single diagnostic character

(the dorsally displaced lateral receptacular clusters on the bursa copulatrix) is also present in species outside the genus, but it is not shared by the closely related species pair "*Songthela*" *australis* and *Heptathela nui* sp. n. The original concept of this genus does anyway no longer correspond to the currently included species apart from the type species, *S. hangzhouensis* (see Platnick, 2011). "*Songthela*" *australis* and "*Songthela*" *cipingensis* Wang, 1989 were transferred to *Heptathela* in an earlier version of Platnick's (2011) online catalogue, without giving an explanation. Three other species [*H. heyangensis* (Zhu & Wang, 1984), *H. schensiensis* and *H. sinensis*, all with a different type of vulva than in the type species] were included in "*Songthela*" by the synonymisation of "*Abcathela*" with "*Sinothela*" and then by the synonymisation of "*Sinothela*" with "*Songthela*".

The generic concept of "*Nanthela*" is also rejected because it is not based on any clear apomorphies. One of the two diagnostic characters, the cymbial projection is also present in species outside "*Nanthela*", e.g., in *H. kikuyai* (Fig. 44), *H. kimurai* (Fig. 46) and "*Sinothela*" *schensiensis* (see Song & Haupt, 1984: fig. 1c-d). The other diagnostic character of "*Nanthela*", the slender conductor, is possibly plesiomorphic (Haupt, 1990: 137, fig. 1; Haupt, 2003: fig. 61, table 11). Instead of retaining this poorly defined genus and transferring species from the well-established genus *Heptathela* to it ("*Songthela*" *australis*, *H. nui* sp. n., "*Nanthela*" *tonkinensis*, *H. to-mokunii* and presumably also other species from Vietnam form a distinct clade), we here place "*Nanthela*" in the synonymy of *Heptathela*.

We want to point out that the systematics of the Heptathelinae (except for the fairly well-defined and monophyletic group of species currently placed in the genus *Ryuthela*), as proposed by Ono (2000), Haupt (2003), Platnick (2011) and summarized in Table 2, are in dire need of a comprehensive revision based on genitalic characters of both sexes, and ideally also on molecular data. Until this is done (and the missing sexes are found), transferring or (in most cases) returning all non-*Ryuthela* Heptathelinae to *Heptathela* solves at least the problem of having closely related species in different genera. This solution is not ideal. *Ryuthela* appears to be an offshoot from within *Heptathela*, leaving the latter paraphyletic. At the moment no other monophyletic groups of species, which are sufficiently distinct to warrant generic rank, can be recognized within *Heptathela*. However, a more comprehensive study including the missing sexes (and new species yet to be discovered) may show that distinct clades do exist in *Heptathela* as defined here. If so, the 34 nominal taxa here included in *Heptathela* could be split into several genera again. In that case plenty of generic names will be available.

SUPPLEMENTARY OBSERVATIONS: *Venom glands and moulting position*: While Haupt's (2003) monograph is a very useful and comprehensive compilation of the knowledge of the Mesothelae of that time, his characterisation of the group includes two misinterpretations:

1) Haupt stated that mesothelid spiders do not possess venom glands ("Mesothelae, however, lack such venom glands. ... This can only mean that venom glands are an apomorphic character of Opisthothelae"; Haupt, 2003: 6), despite the detailed description and illustration of such a gland in *Liphistius desultor* Schiödte, 1849 by Millot (Bristowe & Millot, 1933: 1046, pl. 3, figs 1-2). This question has now

TABLE 2. Different generic placements of species of non-*Ryuzhela* Heptathelinae in the original description, in two fairly recent publications establishing additional genera, in an online catalogue and in the present paper. 1 = species originally described as subspecies. — = species name not mentioned in the corresponding publication. Genus names between inverted commas are currently in synonymy.

Species	Original generic placement	Placement in Ono, 2000	Placement in Haupt, 2003	Placement in Platnick, 2011	Placement in present paper
<i>abca</i> Ono, 1999	<i>Heptathela</i>	" <i>Abcathela</i> "	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>amamiensis</i> Haupt, 1983 ¹	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>australis</i> Ono, 2002	" <i>Songthela</i> "	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>bristowei</i> Gertsch, 1967	<i>Heptathela</i>	" <i>Abcathela</i> "	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>ciltensis</i> Yin, Tang & Xu, 2003	<i>Heptathela</i>	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>cipingensis</i> Wang, 1989	<i>Liphistius</i>	" <i>Songthela</i> "	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>cucphuongensis</i> Ono, 1999	<i>Heptathela</i>	" <i>Vinathela</i> "	<i>Liphistius</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>goulouensis</i> Yin, 2001	<i>Heptathela</i>	—	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>hangzhouensis</i> Chen, Zhang & Zhu, 1981	<i>Heptathela</i>	" <i>Songthela</i> "	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>heyangensis</i> Zhu & Wang, 1984	<i>Liphistius</i>	" <i>Abcathela</i> "	" <i>Smothela</i> "	" <i>Songthela</i> "	<i>Heptathela</i>
<i>higoensis</i> Haupt, 1983 ¹	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>hongkong</i> Song & Wu, 1997	<i>Heptathela</i>	" <i>Vinathela</i> "	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>hunanensis</i> Song & Haupt, 1984	<i>Heptathela</i>	" <i>Nanthela</i> "	<i>Heptathela</i>	" <i>Nanthela</i> "	<i>Heptathela</i>
<i>jiangnanensis</i> Chen, Gao, Zhu & Luo, 1988	<i>Heptathela</i>	" <i>Abcathela</i> "	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>kanemai</i> Ono, 1998	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>kikuyai</i> Ono, 1996	<i>Heptathela</i>	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>kimurai</i> Kishida, 1920	<i>Liphistius</i>	—	—	—	<i>Heptathela</i>
<i>luotianensis</i> Yin, Tang, Zhao & Chen, 2002	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>mangshan</i> Bao, Yin & Xu, 2003	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>nishikawai</i> Ono, 1998	<i>Heptathela</i>	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>nui</i> sp. n.	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>sapana</i> Ono, 2010	" <i>Abcathela</i> "	—	—	—	<i>Heptathela</i>
<i>schensiensis</i> Schenkel, 1953	<i>Liphistius</i>	" <i>Abcathela</i> "	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>shei</i> Xu & Yin, 2001	<i>Heptathela</i>	—	<i>Heptathela</i>	" <i>Songthela</i> "	<i>Heptathela</i>
<i>sinensis</i> Bishop & Crosby, 1932	<i>Heptathela</i>	" <i>Abcathela</i> "	" <i>Smothela</i> "	<i>Heptathela</i>	<i>Heptathela</i>
<i>suoiyuiensis</i> Yin, Tang & Xu, 2003	<i>Heptathela</i>	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>tomokunii</i> Ono, 1997	<i>Heptathela</i>	—	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>tonkinensis</i> Bristowe, 1933	<i>Liphistius</i>	" <i>Vinathela</i> "	" <i>Nanthela</i> "	" <i>Nanthela</i> "	<i>Heptathela</i>
<i>wosanensis</i> Wang & Jiao, 1995	<i>Heptathela</i>	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>xianmingensis</i> Yin, Tang, Zhao & Chen, 2002	<i>Heptathela</i>	—	—	<i>Heptathela</i>	<i>Heptathela</i>
<i>yagimurai</i> Ono, 1998	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>yakushimaensis</i> Ono, 1998	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>yanbaruensis</i> Haupt, 1983 ¹	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>
<i>yunnanensis</i> Song & Haupt, 1984	<i>Heptathela</i>	" <i>Abcathela</i> "	<i>Heptathela</i>	<i>Heptathela</i>	<i>Heptathela</i>

been settled by Foelix & Erb (2010a: 7-8, fig. 10; 2010b), who show that extant mesothelid spiders (at least females and juveniles) have venom glands. In liphistiid spiders the venom probably does not play an important role during prey capture. Upon seizing prey, the spiders almost immediately start crushing it with their strong and unusually mobile chelicera, which can be spread at a right angle to each other. *Liphistius* bites to one of us (PJS) had no recognizable toxic effects.

2) He also stated that "the moulting specimen turns round and lies on its back for the moulting process ..." (Haupt, 2003: 49-50, 95), in the same way as theraphosid spiders do, and he concludes "As this turning for moulting does not occur in other Megoperculata ... it seems to be an autapomorphic habit characteristic of Araneae" (Haupt, 2003: 50). This is not the case. Haupt was presumably generalizing from a single observation captured in a photo (Haupt, 2003: fig. 35D) which shows the final moult of a *L. trang* Platnick & Sedgwick, 1984 male lying on its back. Looking at the exuvia in this photo, however, it becomes clear that the spider actually moulted in a venter-down position. When pulling the anterior limbs out of the old cuticle, the posterior legs obviously remained stuck in it. As the spider struggled to get free, both legs IV and one leg III (still soft and flexible) bent backwards and the spider fell on its back. The damage to the discarded exuvia seen in another photo (Haupt, 2003: fig. 35E), with the fourth pair of legs missing, clearly show that this was not a normal moult and that the spider's fourth pair of legs probably got permanently stuck in the exuvia. An examination of this specimen in Haupt's collection should confirm our interpretation. We have had the chance to observe dozens of moults of liphistiid spiders in captivity, and we have collected hundreds of exuviae in the field and in captivity. In all cases the exuviae were in a venter-down position, with the leg claws and palpal claws gripping the substrate (Figs 65-66). In the interior of their burrows (in nature liphistiids always moult inside them) there is not enough space for the spiders to arch up and bend backward during moulting. They thus normally moult in the same position as uropygids and amblypygids.

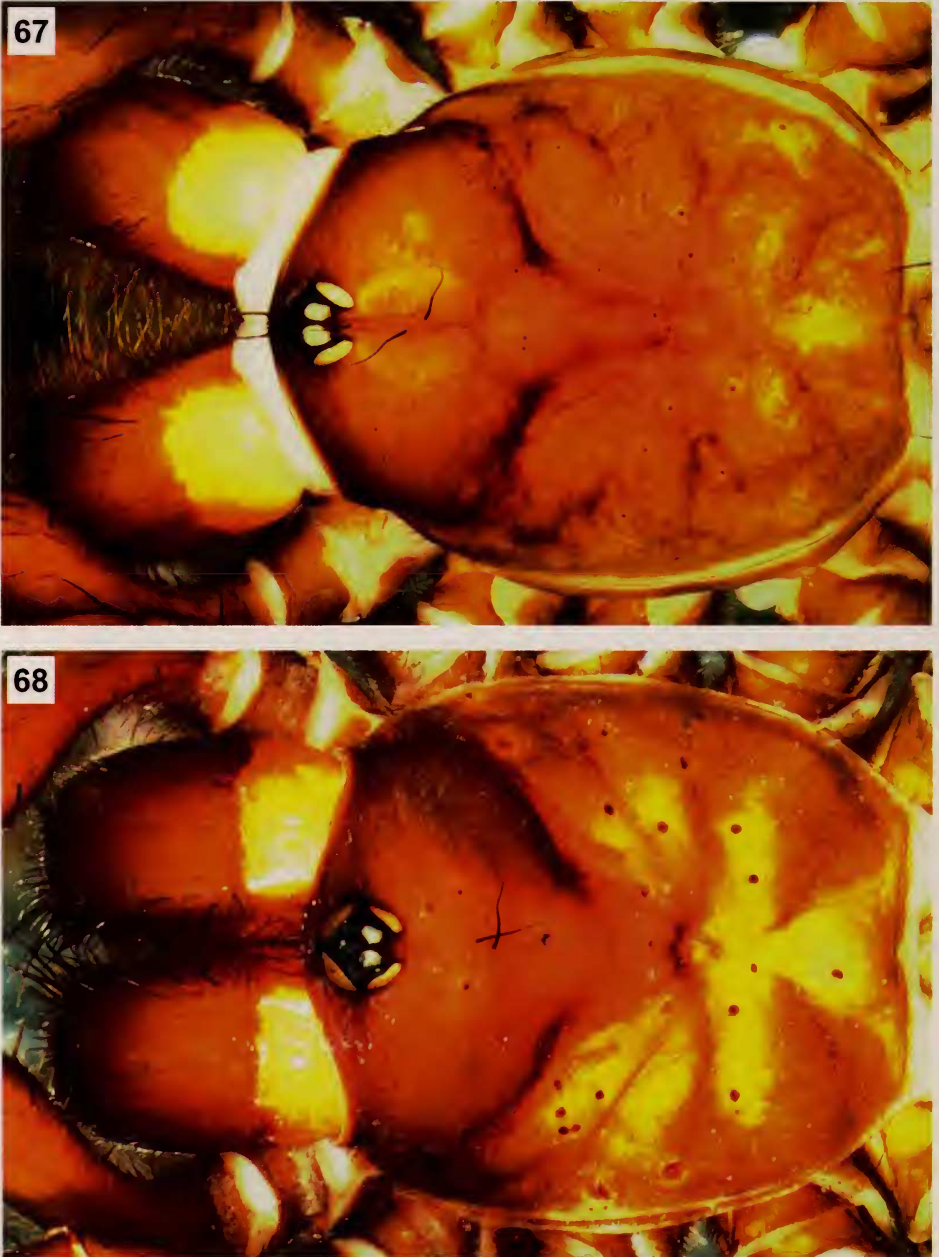
Ectoparasitic mites: The same kind of mites, as were collected from the two *Heptathela* species in southern Vietnam (Figs 67-68 show bite marks), were also found on *Liphistius* at several localities in Laos, Thailand and peninsular Malaysia. At one locality in eastern Thailand the majority of liphistiid spiders collected were carrying mites. They stay on their hosts permanently and pierce the hard carapaces and chelicerae but not the soft membranes. These mites were identified as belonging to the laelapid genus *Ljunghia* and are currently being studied by I. Juvara-Bals & B. Halliday. *Ljunghia* includes obligate ectoparasites which naturally occur on primitive spiders in SE-Asia and Australia (Domrow, 1975), and which were also found on a Central American theraphosid spider in captivity (Moraza *et al.*, 2009). So far only one *Ljunghia* species associated with liphistiid spiders is known, *Ljunghia bristowi* (Finnegan, 1933) living on *Liphistius malayanus* in peninsular Malaysia (Finnegan, 1933). Further species, including the one living on *H. australis* and *H. nui* sp. n., will be described soon.

It appears worth pointing out that all *Heptathela* specimens from southern Vietnam that carried such mites were reproducing females that either laid eggs (3 *H. australis*) or were gravid (1 *H. nui* sp. n.). No mites were seen on juveniles or mature



FIGS 65-66

Liphistius sumatranus Thorell, 1890, moulting of an immature male in captivity. (65) Spider partly emerged from the old cuticle. (66) Spider fully emerged. Note that the animal does not lie on its back.



FIGS 67-68

Dorsal view of prosomata of two females showing bite marks caused by ectoparasitic *Ljunghia* mites. (67) *Heptathela australis* (Ono, 2002); chelicerae spread due to preservation. (68) *H. nui* sp. n., paratype; chelicerae in normal position.

males. This may just be a coincidence, because in *Liphistius* such mites were also found on females that did not reproduce in captivity, and on immature and mature males (unpublished observation).

ACKNOWLEDGEMENTS

The MHNG supported the first author's collecting trip to southern Vietnam. The Japan Society for the Promotion of Science (JSPS No. 21540487) supported the second author's study. Christine Rollard (MNHN) kindly sent us the holotype of *Heptathela tonkinensis* for examination. Ilinca Juvara-Bals (Cologne, Switzerland) identified the mites; Bruce Halliday (CSIRO, Canberra, Australia) confirmed her identification and provided additional information. Rainer Foelix (Aarau, Switzerland) pointed out the cuticular bases of the receptacular glands and commented on the ultrastructure of spider genitalia. Norman Platnick (American Museum of Natural History, New York, USA) kindly reviewed the manuscript and pointed out hypotheses and publications that we have overlooked. Yoshimi Watanabe (NSMT) produced most of the ink drawings, Christina Lehmann-Graber (MHNG) completed them and added other ones, André Piuz (MHNG) took the SEM micrographs, Florence Marteau and Lionel Monod (both MHNG) arranged all illustrations into plates. John Hollier (MHNG) checked the English text and suggested improvements. The Bulletin of the National Science Museum (Tokyo), renamed the Bulletin of the National Museum of Nature and Science, allowed us to reproduce figures 51-54 from Ono & Schwendinger (1990).

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